Abstract

RESPONSES OF DOMINANT MARSH MACROPHYTES
TO INUNDATION AND DISTURBANCE
AND ASSESSING MARSH ECOSYSTEM SERVICES

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Within two hydrodynamically different inundation regimes in North Carolina, the growth response and interactions of two dominant marsh macrophytes were evaluated over a range of inundation periods to understand better how coastal marshes will respond to rising sea levels. Marsh vegetation is likely key to accretion processes. Greater aboveground biomass baffles floodwaters, potentially increasing sedimentation, and greater belowground biomass contributes directly to the elevation of marsh substrate. Multi-level planters were used to evaluate experimentally the response of *Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele to an array of inundation periods. Groundcover changes were evaluated before and after a pulsed disturbance to simulate conditions where these species are naturally delineated on the marsh platform. Peak production of *S. alterniflora* and *J. roemerianus* occurred at inundation periods of 0.5 to 14% and 0.4 to 28%, respectively, in marsh planters. The growth response patterns of *S. alterniflora* and *J. roemerianus* to inundation period were similar, although *J. roemerianus* appeared to experience greater stress in an astronomically-dominated than in a meteorologically-dominated inundation regime. *Spartina alterniflora* was found to be more resilient to disturbance than *J. roemerianus* in planters and on the marsh platform.

Sixteen months following a one-time cutting disturbance, a significant decline in *J. roemerianus* and encroachment of *S. alterniflora* in experimental platform plots was observed within both regimes. Estuarine inundation appears to function as both a subsidy and stressor to marsh macrophytes. I propose a conceptual model to describe this relationship.

The scaling of the losses and gains in marsh ecosystem services is reviewed within the context of coastal marsh habitat injury, restoration and creation as achieved by the Natural Resource Damage Assessment and compensatory restoration processes. An analysis into the current methods used to assess ecosystem services found that U.S. statutes provide for the compensation of loss of public trust resources, yet current metrics for ecosystem services serve as incomplete proxies of ecosystem function and condition. Coastal ecosystems have and will transgress in response to rising sea levels. Data from this investigation suggest that marsh accretion is challenged by increased inundation rates, especially where sediment supplies are limiting, thus, highlighting the need for accommodating transgression within the coastal zone.

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Christine M. Voss

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1. INTRODUCTION

Overview

Accelerated rates of sea-level rise (SLR) are among the most important responses to global climate change phenomena affecting Earth's coastal zones. The IPCC (2007) estimates that eustatic sea level will rise 0.2-0.6 m by 2100. Projections that are more recent conclude that the IPCC's estimate is likely too low and suggest that a rise of 0.5-1.4 m (Rahmstorf 2007), 0.9-1.3 m (Grinsted et al. 2009) or even 0.8-2.0 m (Pfeffer et al. 2008) are more likely by 2100. All projections acknowledge the substantial uncertainties associated with glacial dynamics in Greenland and Antarctica, yet the agreement and degree of overlap in more recent estimates suggest these are the general conditions for which we should prepare. Rising sea level has worldwide consequences because of its potential to alter ecosystems and even human occupation of coastal regions. In the USA, approximately half of our nation's population is concentrated along the coastal zone (Crossett et al. 2004), and the range and magnitude of impacts resulting from sea-level rise are immense and unprecedented. Because rising sea level is a relatively gradual process, proactive management strategies have the potential to determine significantly the viability and sustainability of coastal zone ecosystems.

The effects of accelerated rates of SLR are already apparent along much of the U.S. Atlantic and Gulf Coasts and may cause the dramatic modification of important coastal ecosystems and loss of some valuable ecosystem services over the next few decades (Kennish 2001, Scavia et al. 2002). Estuarine shorelines are under the stress of increased water levels ranging from short-term waves and storm surge to long-term

inundation through increased rates of SLR. In areas where shorelines or wetlands must migrate inland to persist, managers must be able to predict the effects of SLR to implement protection or retreat strategies to reduce the hazardous and negative economic impacts of inundation and shoreline movement.

Relative sea-level rise (RSLR) (eustacy, steric effects plus local and regional processes affecting elevation) continues to alter the North Carolina coast. Regional assessments of sea-level trends in North Carolina have suggested the rate of rise was 4.3 mm yr^{-1} for most of the 20^{th} century (Poulter 2005) and has ranged from 2.04 mm yr^{-1} at Southport to 4.27 mm yr^{-1} at Duck (Zervas 2004). Recent work by Kemp et al. (pers. comm., 2009) estimated that RSLR rate in North Carolina was 0.98 mm yr^{-1} (±0.40 mm yr^{-1}) from the period of 1000 B.C. to 1850 A.D. and dramatically increased since 1850 to 4.74 mm yr^{-1} (±0.02 mm yr^{-1}), based upon analyses of microfossils and carbon dating of peat cores. These rates compare with a eustatic mean SLR rate of 1.8 mm yr^{-1} for the past century (Douglas 1997, Church and White 2006) and a recent mean rate of 3.1 mm yr^{-1} from 1993-2003 (Bindoff et al. 2007). Sea-level rise and the acceleration of SLR contribute to a suite of stressors currently impacting our coastal ecosystems. Coastal marshes are among the ecologically and economically valuable ecosystems in jeopardy from accelerated SLR and anthropogenic coastal zone alterations; to date, these marshes have persisted through centuries of RSLR by processes such as vertical accretion and landward horizontal migration (transgression).

The coast of North Carolina encompasses marsh habitat with two distinctly different hydrologic regimes within practical geographical proximity. Marshes that are

located near inlets along the eastern rim of the coastline and within sounds and estuaries well connected to the ocean experience astronomically-driven (semi-diurnal) tidal regimes. Marshes positioned away from inlets or within the sounds and estuaries with restricted access to the ocean, such as along the western shore of the Pamlico Sound, experience meteorologically-driven (micro-tidal) hydrologic regimes with minimal astronomical tides. These relatively unique geographic features provide an excellent opportunity for the study of the effects of the range of hydrologic regimes that marshes will experience along the U.S. Atlantic and Gulf Coasts due to RSLR. Accelerated RSLR is expected to result in increased tidal amplitude and salinity in areas that are currently meso- and micro-tidally inundated; this may affect changes in plant community composition in the coastal wetlands. *Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele are the dominant macrophytes of tidal and irregularly flooded southeastern U.S. marshes, respectively (Mitsch and Gosselink 2000).

Marsh ecosystems may have evolved to be resilient to natural stressors; on smaller scales press (e.g., sea-level rise) and pulse (e.g., wrack deposition) disturbances (Bender et al. 1984) act to alter community structure and perhaps initiate changes in ecosystem state. Ecosystem state change is a sequential transformation process whereby an ecosystem state, at a fixed geographic point, is transformed to another state or habitat type due to abiotic forces (Brinson et al. 1995, Hayden et al. 1995). For example, as sea-level rises in a coastal setting, upland forest is converted to high marsh, high marsh to low marsh and low marsh sub-tidal flat. Ecogeomorhpological position influences community stability, as well as the nature of the subsidies and stressors experienced by a

given community within the larger ecosystem (Keusenkothen and Christian 2004). Among other effects, sea-level rise effectively increases the hydraulic head of the estuary and thus logically results in a decrease in upland and high marsh drainage (as per LaRoche and Webb 1987, Titus et al. 1987, Waddell and Blaycock 1987). Consequently, this lack of drainage from high marsh areas can result in hydraulic isolation within marsh ecosystems in areas not influenced by tidal pumping. Increasing water levels will gradually transform the hydrogeomorphic settings within marshes, promoting a shift in ecosystem state; however, transitions in state may be accelerated by pulse disturbances (Brinson et al. 1995). While the response of coastal marshes to an increased rate of RSLR is uncertain, the societal need for marsh ecosystem goods and services is unending. Hence, understanding the response of marsh ecosystems to RSLR is crucial for successful management of the coastal zone.

The ecological functions intrinsic to the world's ecosystems provide an array of services to humans (Daily et al. 1997, de Groot et al. 2002, MEA 2005, NRC 2005). Ecological services support the interrelated functions of natural communities and support many human enterprises and values (CESR 2008). The contributions of these services are often undervalued and are not fully recognized until ecosystem condition or function is reduced or eliminated. Consequently, environmental insults to public natural resources and the ecosystems they support were long accepted without requiring compensation. In the United States, numerous federal policies and legislative acts have recognized the wisdom of preserving critical ecosystem services provided by public trust resources and have established requirements for the compensation of environmental injuries. For

example, the federal Clean Water Act (Section 404) requires that construction projects avoid, then minimize where unavoidable, and finally mitigate any remaining damage to wetlands. The "no net loss" concept for wetlands was developed by the National Wetlands Policy Forum (published in 1988), a stakeholder panel brought together by the Conservation Foundation, with the short-term goal of no net loss and a long-term goal of a net gain in US wetland area, function and value. Coastal marshes are valued, protected, and restored in recognition of the comprehensive suite of their ecosystem services: (1) high productivity and habitat provision supporting the foodweb leading to fish and wildlife (Teal 1962, Weisberg and Lotrich 1982, Boesch and Turner 1984, Peterson and Turner 1994, Minello et al. 2003), (2) buffer against storm wave damage (Mitsch and Gosselink 2000), (3) shoreline stabilization (NCDCM 2006), (4) flood water storage (Mitsch and Gosselink 2000), (5) water quality maintenance (Stone et al. 1990, Correll et al. 1992), (6) biodiversity preservation (Keer and Zedler 2002; Callaway et al. 2003), (7) carbon storage and biogeochemical cycling (Mitsch and Gosselink 2000, Chmura et al. 2003, Brevik and Homburg 2004, Choi and Wang 2004) and (8) socio-economic benefits (Mitsch and Gosselink 2000, MEA 2005). Sustaining ecosystem function and condition allows ecosystem services to perpetuate across space and time to benefit humans both directly and indirectly. Natural processes and anthropogenic actions that reduce function or condition, reduce the level of goods and services available to societies. Coastal policy can address the natural geomorphological evolution and manage social exploitation of ecosystems with the goal of sustainability. The authority to seek compensation for natural resource damages under federal and state statutes has led to new fields of study

such as restoration ecology. Resource managers throughout the country, and increasingly throughout the world, rely on a wide selection of methods to determine the appropriate quantity and type of restoration to compensate for perturbations to ecological resources and systems. Methods to "scale" (measure and balance) restoration actions to equate to the interim loss of injured public trust resources combine techniques from the fields of ecology and economics. Determining just restoration measures and public compensation for resource injuries necessitates a sound knowledge of ecosystem function and condition as well as an improved understanding of the flow of services to societies.

The research on which this dissertation was funded largely by a grant from the National Centers for Coastal Ocean Science's Center for Sponsored Coastal Ocean Research, part of the National Oceanic and Atmospheric Administration's National Ocean Service (NOAA) (Grant # FNA05NOS4781184). The basic research within this dissertation contributes to mathematical models with the objective of understanding and predicting the ecological and morphological responses to sea-level rise. Our research team is focused on the morphological evolution of coastal marshes in response to tidal forcing and sea-level rise. This team included geologists from Vanderbilt University (David J. Furbish and Susan M. Howell) and the U.S. Geodetic Survey (Donald R. Cahoon) and ecologists from East Carolina University (Robert R. Christian) and the University of South Carolina (James T. Morris); Dr. Morris.

As part of the Coastal Resources Management program requirements, I served as team member on a project for the Coastal Response Research Center (CRRC), a partnership between NOAA and the University of New Hampshire. Briefly, the CRRC is

focused on developing new approaches to hazardous-material-spill response and restoration in marine and estuarine ecosystems through research and synthesis of information. The result of our project was a book, *Ecology and Economics of Restoration Scaling*, which is a synthesis of restoration scaling methods used in coastal ecosystem damage response and restoration. I was invited to join an ecologist, Dr. C. H. Peterson and an economist, Eric English, who have each had experience in the assessment, scaling, restorative planning necessitated by discrete ecosystem damage incidents, as they relate to the Comprehensive Environmental Response, Compensation, and Liability Act (CERCLA) and Oil Protection Act (OPA). As a collaborator, I focused on aspects of damage assessment, scaling, and restoration of coastal habitats and the replacement of ecosystem services that are held in the public trust. Details of this work, as it pertains to coastal marsh ecosystems, are discussed in chapter four.

The main objectives of this dissertation are:

1) To determine the growth response (aboveground/belowground biomass and productivity) and tolerance limits of dominant marsh macrophytes to inundation period (*Spartina alterniflora* and *Juncus roemerianus*) and inundation regime (*Juncus roemerianus* only)
2) To elucidate interactions between *Spartina alterniflora* and *Juncus roemerianus* with respect to inundation period and disturbance
3) To review the scaling of the losses and gains in marsh ecosystem services within the context of the injury, restoration and creation of coastal marsh habitat as achieved in the Natural Resource Damage Assessment process.

Dissertation organization

This dissertation is structured with two summary chapters at the beginning (this introduction) and end (synthesis) that encase two chapters of original research prepared as manuscripts to be submitted as primary literature and a review chapter suitable for a coastal management journal. Each of the core chapters is written to be published individually and is formatted for the target journal. A brief summary of each chapter is given below.

In chapter 2, I investigate the growth response of two dominant marsh macrophytes, *S. alterniflora* and *J. roemerianus*, to inundation period within each of the two chief hydrodynamically different inundation regimes found in North Carolina. *Spartina alterniflora* and *J. roemerianus* are among the dominant macrophytes of tidal and brackish, irregularly flooded marshes, respectively, along the Mid-Atlantic, South Atlantic and Gulf Coasts (Eleuterius 1976, Mitsch and Gosselink 2000); coastal marshes in these regions comprise approximately 90 % of the U.S. total (NOAA 1990, Watzin and Gosselink 1992). Morris et al. (2002) have demonstrated that the relative elevation, and thus, inundation period, of the sediment surface is a critically important variable that controls the productivity of the salt marsh vegetation, and that macrophyte productivity has a positive feedback on the rate of accretion of the marsh surface. Hence, understanding of the response of marsh macrophytes to inundation is essential to the broader understanding of coastal wetland response to the higher water levels and tides associated with rising sea level, and for predicting changes in the geomorphology of the estuarine shoreline. In this chapter, I employ the term "we" to include my intended co-

authors, Dr. Robert R. Christian and Dr. James T. Morris, of a manuscript we plan to submit to *Ecological Applications*, a peer-reviewed journal of the Ecological Society of America.

In chapter 3, I explore the interrelationships of *S. alterniflora* and *J. roemerianus* over a range of inundation periods in each of distinct inundation regimes. In this study, I focus on the species-level response at the *J. roemerianus*-*S. alterniflora* marsh interface to extrapolate how processes at the community level might offer insight into the transformation of a high marsh state to a low marsh state. In addition, I explore the effects of disturbance on community structure along the *J. roemerianus*-*S. alterniflora* margin where an abrupt delineation of these dominant macrophytes occur.

In chapter 4, I review the methods employed for the assessment of coastal marsh ecosystem services that are commonly used in natural resource damage assessment and compensatory restoration cases. Under US federal statutes, natural resource trustees are authorized to act on behalf of the public to protect the resources of the Nation's environment (NOAA 1997, Burlington 1999, NRC 2001). Together, federal, state and sometimes local or tribal trustees of coastal and marine resources determine the damage claims to be filed against parties responsible for injuries to natural resources resulting from discharges of oil, releases of hazardous substance or physical injury such as vessel groundings. The scaling of ecosystem services is a methodology for qualifying and quantifying ecosystem services for this purpose and draws on a variety of techniques from the fields of ecology and economics. Marsh ecosystems are recognized for providing a wealth of ecosystem services within the world's coastal zones (Boesch and

Scavia 2000, MEA 2005, Peterson et al. 2008). The contributions of these services are often not fully recognized until ecosystem function is reduced or eliminated. A key challenge to those responsible for the management of public trust resources is the scaling of the ecosystem services provided by these natural resources.

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Chapter 2. RESOLVING MARSH MACROPHYTE RESPONSE TO INUNDATION

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ABSTRACT

The growth response of two dominant marsh macrophytes was examined over a range of inundation periods to understand how coastal marshes will respond to rising sea levels. Marsh vegetation is likely key to accretion processes. Greater aboveground biomass baffles floodwaters potentially increasing the degree of sedimentation; and greater belowground biomass contributes directly to the elevation of marsh substrate. In North Carolina, multi-level planters were employed to evaluate experimentally the response of *Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele to an array of inundation periods. Significant trends of decreasing above- and below- ground growth with increasing inundation were observed across most response variables. Peak production of *S. alterniflora* and *J. roemerianus* occurred at inundation periods of 0.5 to 14% and 0.4 to 28%, respectively, in marsh planters. Essentially no seasonal increase in *S. alterniflora* or *J. roemerianus* biomass was observed at elevations inundated ≥ 67 % and ≥ 42 to 53 %, respectively. The growth response patterns of *S. alterniflora* and *J. roemerianus* to inundation period were similar; though, *J. roemerianus* appeared to experience greater stress in an astronomically-dominated than in a meteorologically-

dominated inundation regime. Estuarine inundation appears to function as both a subsidy and stressor to marsh macrophytes. We propose a conceptual model to describe this relationship.

INTRODUCTION

Coastal marshes are among the ecologically and economically valuable ecosystems in jeopardy from the acceleration of sea-level rise (SLR) (Scavia et al. 2002, IPCC 2007, Rahmstorf 2007, Peterson et al. 2008a); yet these wetlands have maintained elevation relative to sea level for millennia (Redfield 1965, 1972, Orson et al. 1987, Reed 2002) through processes such as vertical accretion and horizontal transgression across the landscape. Marsh accretion occurs through the mechanisms of sedimentation (from estuarine sources) (Leonard and Luther 1995, Leonard et al. 1995, Reed 2002) and bioaccretion (accumulated organic matter in marsh substrate) (Cahoon et al. 1998, Turner et al. 2000, Blum and Christian 2004, Nyman et al. 2006). Ultimately, it is the intimate relationship of marsh surface elevation (relative to sea level), marsh hydrology (chiefly estuarine inundation) and macrophyte response that determines the persistence of marsh ecosystems. Early models predicted that intertidal marshes approach an equilibrium elevation that approximates that of mean high water (MHW), suggesting that the quantity of sediment deposited on the marsh surface is proportional to the water depth inundating the marsh (Krone 1985). Morris et al. (2002) have demonstrated that the relative elevation, and thus, inundation period, of the sediment surface is a critically important variable that controls the productivity of the salt marsh vegetation and that macrophyte productivity has a positive feedback on the rate of accretion of the marsh surface. Hence, understanding of the response of marsh macrophytes to inundation is essential to the broader understanding of coastal wetland response to the higher water levels and tides

associated with rising sea level, and for predicting changes in the geomorphology of the estuarine shoreline.

Spartina alterniflora Loisel and *Juncus roemerianus* Scheele comprise the dominant vegetation (Eleuterius 1976, Mitsch and Gosselink 2000) in 90% of U.S. coastal marshes (NOAA 1990, Watzin and Gosselink 1992) over a wide range of inundation regimes. An increasing rate of relative SLR (RSLR), the cumulative effects of eustatic SLR, steric effects and local and regional processes affecting elevation, are expected to result in increased tidal amplitude and salinity in areas that are currently minimally or irregularly inundated (Pethick 1993, Rosenzweig et al. 2007). This change in inundation regime will likely effect changes in community composition and is predicted to result in ecosystem state changes (Brinson et al. 1995) within the coastal zone. *Spartina alterniflora* occurs along the lowest terrestrial elevation along estuarine shorelines, characteristically dominating the intertidal zone, and it decreases aboveground production and its ability to dominate at higher elevations where flooding is less regular (Bertness and Pennings 2000) and its elevational distribution increases with increasing mean tidal range (McKee and Patrick 1988). Primary production for *S. alterniflora* varies with distance from shoreline across the marsh surface and production is usually greatest along the marsh-estuarine interface (Nixon and Oviatt 1973, Gallagher 1974, Broome et al. 1975, Turner 1976, Pomeroy et al. 1981, Howes et al. 1986), zones that typically receive greatest inundation. *Juncus roemerianus* tends to dominate at slightly higher elevations under irregularly flooded conditions, but it can be found in areas of more regular flooding (Woerner and Hackney 1997, Brinson and Christian 1999). In

Georgia salt marshes and transplant experiments, Pennings et al. (2005) showed that *J. roemerianus* was limited by physical stresses (flooding and salinity) at its seaward boundary and not by competition, whereas, *S. alterniflora* at its landward boundary was limited by competition with *J. roemerianus*. In South Carolina, Morris and Haskin (1990) found that *S. alterniflora* primary production positively correlated with site-specific mean sea level and rainfall. Thus it appears that the growth response of *S. alterniflora* and *J. roemerianus* differ with inundation period (% time flooded) or inundation regime (flooding pattern, e.g., tidal or irregular), but direct comparative evidence is limited.

Numerous studies have investigated the effects of inundation on the production of *S. alterniflora* (Steever et al. 1976, Odum 1979, McKee and Patrick 1988, Morris et al. 1990, Morris and Haskin 1990, Pennings et al. 2005); few have investigated the effects of inundation on the production of *J. roemerianus* (Stout 1978, Christian et al. 1990, Pennings et al. 2005). Elevation largely determines edaphic conditions for marsh macrophytes and has been proposed to be a key determinant of macrophyte net primary production (Mendelssohn and Morris 2000, Morris 2007). Most studies have been observational and based on in situ measurements. One method developed to isolate, manipulate and evaluate the effect of inundation on marsh vegetation is the multi-level planter. The multi-level planter utilized replicate PVC pipes positioned vertically as "pots" over generally a 1-m range in elevation. Multi-level planters have been employed effectively to alter and expand the elevation (thus, the degree of inundation) at which marsh vegetation grows within a given marsh habitat, allowing one experimentally to

examine the growth response of marsh macrophytes over a range of elevations relative to mean sea level (Morris 2007). Several investigations have attempted to elucidate the mechanisms that drive intra-marsh variability in the production and height of *S. alterniflora*. While such research radiates along several lines of causality, we focus on the role of inundation and its subsequent effect on edaphic conditions. Some studies have found *S. alterniflora* production to be positively correlated with elevation such as on berms near tidal creeks (Gallagher 1980, Pomeroy et al. 1981), while others have found it to be positively correlated to inundation (Morris and Haskin 1990, Morris et al. 2002).

The objective of this study was to determine the growth response of the two key dominant marsh macrophytes (*S. alterniflora* and *J. roemerianus)* to a range of inundation periods, to determine their inundation tolerance and to distinguish differences in the growth response of *J. roemerianus* with inundation regime. Because *S. alterniflora* and *J. roemerianus* dominance is sometimes associated with the regularity of inundation pattern, planters containing *J. roemerianus* were deployed at two geographically-proximal marsh sites that experience different inundation regimes, one of which experiences a semi-diurnal, astronomically-dominated inundation pattern and one that experiences an irregular, meteorologically-dominated inundation pattern. We know of no other studies to employ inundation regime as a variable to explain macrophyte growth response. Based upon the current body of knowledge, one would expect overlap in the growth response of dominant macrophyte species to inundation period. We hypothesized that *Spartina* would show more vigorous growth than *Juncus* at most-inundated elevations, and that *Juncus* would show more vigorous growth under a

meteorologically-dominated inundation regime than under an astronomically-dominated inundation regime, given similar inundation periods.

METHODS

Site Description

The North Carolina (NC) coast of the U.S.A. is classified as a micro–tidal system with a tidal range of ~ 1.0 m along the ocean shoreline and inlets, decreasing to a negligible (< 10 cm) astronomical tidal signal along the landward areas of its large sounds which occur in the northern province of the state (Currituck, Roanoke, Albemarle and Pamlico Sounds). The sounds in NC's southern province (e.g. Back, Bogue, Topsail, Middle, Masonboro, etc.) are significantly smaller with more numerous inlets that provide great connectivity to the Atlantic Ocean and are thus dominated by astronomical forces. Overall, the influence of meteorological factors dominates where astronomical influence diminishes (Mukai et al. 2002).

Research sites were established along the central NC coast at two points that differed in hydrodynamic regime. One site was chosen in the southern province at Pine Knoll Shores (PKS) (33.6953N, 76.8417W) and one in the northern province at Lola (LOLA) (34.9501N, 76.2796W); sites were spaced approximately 50 km apart and experienced similar meteorological conditions (Figure 2.1). The astronomical tidal range was measured as 60 cm and 8 cm for PKS and LOLA, respectively. The dominance of the astronomical tidal signal at PKS is responsible for a regular, semi-diurnal pattern of marsh inundation, although meteorological factors (chiefly wind) are also important. The weak astronomical tidal signal experienced at LOLA results in an irregular pattern of marsh inundation; here, the marsh platform is sometimes dry or flooded for weeks at a time. Typically, the marsh experienced less wave energy at the LOLA site than at the

PKS site. The mean annual salinity was 34 (±1.8) psu and 29 (±4.3) psu at PKS and LOLA, respectively.

While low-topographic, erosional geomorphology is common among the research areas, the PKS research site was established on broad, gradually ramping, back-barrier marsh habitat within a dune-and-swale system with few tidal creeks, and the LOLA site was established within an alcove of broad-platform marsh habitat. *Spartina alterniflora* (hereafter, *Spartina*) and *Juncus roemerianus* (hereafter, *Juncus*) were each dominant in a mosaic of patches at each site, with *Spartina* dominating the overall estuarine shore zone at PKS.

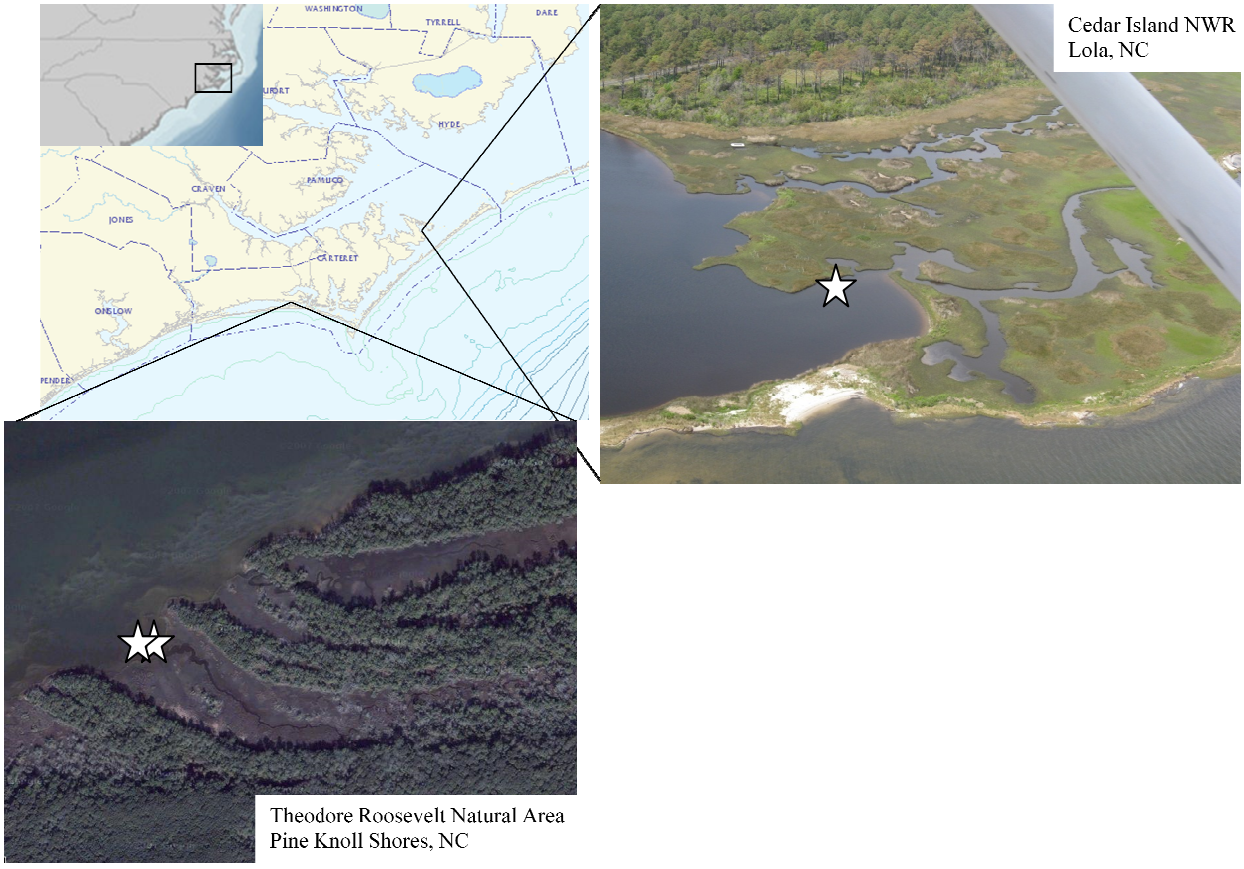


Figure 2.1. Map of NC study area and aerial photo of research sites (stars = marsh planter locations)

Water level record

At each research site, a temporary water level station was established in accordance to the requirements of the National Oceanic and Atmospheric Administration's (NOAA) Center for Operational Oceanographic Products and Services (CO-OPS) (NOAA 2003, NOAA 2007). The PKS station (34.53436^{o}N 76.83176^{o}W) was established at the dock pier of the NC Aquarium in May 2006, and LOLA station (34.95098^{o}N 76.28112^{o}W) was established at the Lola Road dock (property of U.S. Fish and Wildlife) in June 2006. The North Carolina Geodetic Survey established Second Order Class 2 benchmarks at each site in the proximity of the water level stations. Each water level station consisted of two HOBO (Onset Computer Corp., model: U20-001-01) pressure transducers, one of which measured barometric pressure and the other measured water-column pressure; date, time, temperature and transducer pressure were recorded every 3 minutes and downloaded monthly using the manufacturer's software. At each download and launch, water level relative to station benchmark was recorded for reference; from this, water level relative to NAVD88 and mean sea level (MSL) was later computed. A calibrated Topcon® Model RL-50A rotating-laser system was used for all leveling at the research sites; a Trimble® 5800 RTK GPS system unit was used to verify elevation of a temporary benchmark at the PKS marsh-planter site in February 2008. Post-processing of water-level data was completed using HOBOware® software adjusting to time-referenced, site-specific barometric pressure. Water levels from an 18-month period, mid-2006 through December 2007, were used to determine inundation regime patterns for each site. Water levels from the time each monitoring station was

established, 20 May (PKS) and 29 June (LOLA), through 17 September 2006 were used to determine inundation periods for marsh planter rows.

Multi-level planters

The relationship between marsh surface elevation and inundation varies with geomorphology. At our North Carolina research sites, marsh geomorphology can be described as a flat platform (i.e., LOLA) or low-topography ramping platform, with a gradual transition of low and steadily increasing elevation with distance from shoreline (i.e., PKS). Howell et al. (2007) found that tidal inundation is a function of elevation and that the force of drag does not cause a delay in inundation (i.e., a *wave*) for at least the first 100 m of distance from shoreline. This evidence allows for the site-specific assumption that a given elevation receives the same degree of inundation regardless of location within the marsh platform (within 100 m of edge) or in the marsh planter, provided that no levee exists. The proportion of hydrological contributions from estuarine, terrestrial and meteorological sources defines the marsh habitat from upland habitat within the shorezone.

Multi-level marsh planters (Morris 2007) were used to manipulate experimentally the elevation (therefore, inundation period) of dominant marsh macrophytes (*Spartina* and *Juncus*) (Figure 2.2). Each marsh planter was constructed of 15-cm-diameter PVC pipe, cut and bolted to result in open-ended "pots" that formed six rows, at 15-cm vertical intervals, ranging from 30 to 105 cm in elevation above the base; there were six replicates per row (Figure 2.2). Planter rows were numbered with row 1 as the most inundated and row 6 as the least inundated. At each site, marsh planters were positioned in the estuary

(lowest row facing south) just beyond the marsh platform so that the elevation of row 4 was approximately equivalent to the mean elevation of the respective macrophyte species on the adjacent marsh platform. At PKS, in 2006, one planter was established with *Spartina* and one with *Juncus*; in 2007, one planter was established with 3 pots of each elevation containing *Spartina* and the other 3 pots of each elevation containing *Juncus*. Here, the 2007 planter was positioned at a lower elevation relative to the 2006 planter, in an attempt to determine the maximum inundation threshold of *Spartina*. At LOLA, in 2006, one planter was established with *Juncus*, analogous to that at PKS. Table 2.1 shows the elevation of each marsh planter row, relative to NAVD88, mean sea level (MSL) and its % of time flooded during each growing season.

In 2006, marsh planters were planted with *Spartina* or *Juncus*, from two similarly positioned source plots in the respective areas of the adjacent marsh platform, on 15 and 16 March and monitored through 15 and 16 September. Likewise in 2007, planters were maintained from 13 and 14 April through 6 and 7 September. Source plots were limited in size to minimize the possibility of picking different genotypes (e.g. Lessmann et al. 1997). Lower sections of the planter pots were filled with local estuarine sand and approximately the upper 30 cm contained the *Spartina* or *Juncus* plugs planted in marsh sediments; all fill materials were obtained locally from the adjacent marsh platform at both sites.

To compare the growth response of *Spartina* and *Juncus* in the marsh planters to that of the adjacent marsh platform, where possible, row-elevation-equivalent plots were established on the platform adjacent to each planter; here, end-of-season aboveground

biomass of macrophytes was measured and processed in parallel with that of the marsh planters in 2006. At PKS, plots were established within *Spartina* that were equivalent in elevation to planter rows 1-4 and likewise within *Juncus* for planter rows 2-4. At LOLA, the marsh platform elevation only differed by ~ 10 cm within the entire study area; therefore, elevation-equivalent plots were established within *Juncus* in three locations for planter row 4.

(a) (b)

Figure 2.2. (a) Multi-level marsh planters at PKS *Spartina* (left) and *Juncus* (right) adjacent to marsh platform and (b) close-up photo of multi-level marsh planter

Response variables

The response of *Spartina* and *Juncus* to inundation regime was evaluated by measuring (per pot): (1) demographics; length live (green) and dead (brown) of each culm (*Spartina*) or leaf (*Juncus*) and number of leaves on each stem for *Spartina* (2007 only), (2) density, (3) start-to-end of season (seasonal change in) aboveground biomass, (4) end-of-season (EOS) aboveground biomass and (5) belowground biomass. The culm (for *Spartina*) / leaf (for *Juncus*) (hereafter, culm/leaf) proportion of green-to-brown (green: brown) served as a proxy for macrophyte health; we assumed that a seasonal or relative decrease in green: brown indicated stress. The amount of measureable brown leaf length on *Juncus* leaves is generally minimal during about mid-August as leaves begin to naturally senesce in NC (Christian et al. 1990); this was not considered a confounding factor when comparing the response of *Juncus* condition by inundation regime. At the beginning of each growing season, the demographics and density of aboveground material was measured. An estimate of initial aboveground biomass was computed by multiplying the initial overall *Spartina* culm or *Juncus* leaf length per pot (demographics data) by the mean mass per culm/leaf length (mass: length) as determined by 78 culms and 117 leaves for *Spartina* and *Juncus*, respectively. A regression of the mass and length yielded a factor of 0.024964 g cm^{-1} (r^2= 0.72, $P< 0.001$, n=78) and 0.010904 g cm^{-1} (r^2= 0.570, $P< 0.001$, n=117) for *Spartina* culms and *Juncus* leaves, respectively. At the end of each growing season, aboveground biomass from each pot was clipped at the soil surface and placed into labeled bags in the field; in the lab, each culm/leaf length was measured (green, brown and total length), culms/leaves counted,

and samples were dried at 85^{o} C until weights were stable. The belowground biomass from each pot was placed into labeled bags in the field. At the lab, samples were first liberated from soil while contained in 1-mm mesh nylon screening using water pressure (hose and nozzle), then samples were sieved (via water pressure) using 5.6-mm and 1-mm mesh sieves to separate "live" (>5.6-mm mesh) and "dead" (>1-mm mesh) material (similar to methods used by Valiela et al. 1976, Gallagher et al. 1988, Darby and Turner 2008). Live and dead belowground fractions were dried and weighed, as were aboveground samples; two sub-samples of each dried fraction were ashed at 500^{o} C for 6 hours to determine organic matter content, thus, belowground biomass data reported here includes only organic matter.

Statistical analyzes

SYSTAT ® software (version 11.00.01) and SAS® software (version 9.1) were used for all statistical analyses. Most metrics met the Shaprio-Wilks criteria for normality (Shapiro-Wilks P≥ 0.10). Consequently parametric statistics were used for all of our statistical analyses. Inundation period (as percent time flooded), our chief independent variable, was normalized by taking the arcsine of the square root of the proportion of time flooded (as per Sokal and Rohl 1981). A General Linear Model (GLM) was used to assess the statistical significance ($\alpha = 0.05$) of the effect of inundation on macrophyte growth response metrics. In some cases, the data indicated a plateau or threshold response to inundation; here, we also report cases where a quadratic model of the data yielded a stronger relationship (higher r^2 value) than a linear fit of the data. Where linear regressions were also relevant, we report the strength (r^2 value) and

significance (P-value) of a given growth response to inundation. Two-sample t-tests were used to compare: (1) growth response variables (EOS aboveground biomass) between the marsh planter and adjacent marsh platform by inundation period at each site, for each species and (2) growth response variable (EOS above- and below-ground biomass, seasonal difference in biomass, density and leaf green: brown) of *Juncus* between inundation regime. Where we report mean values for treatments, we follow with the standard error of the mean (SEM) in parentheses. Some of the 2006 *Spartina* aboveground biomass samples were destroyed inadvertently prior to analysis, and four samples were lost from marsh planters (one in 2006 and 3 in 2007), Table 2.3 specifies sample size.

RESULTS

Water levels

The 18-month water level record revealed distinct differences and patterns between the two research sites (Figure 2.3). Here, the chief harmonic constituents (M_2, K_1, O_1 and solar annual) explained 59% and 23 % of the observed water level at PKS and LOLA, respectively. It is assumed that meteorological effects explicate the majority of balance of unexplained water levels (i.e., 41 % and 77% for PKS and LOLA, respectively).

PKS . At PKS, the difference between MSL and MHW was approximately 0.30 m and MSL is 0.118 m below NAVD88. In 2006, the *Spartina* marsh planter rows were submerged 81, 57, 28, 14, 3 and 0.5 percent of the growing season for rows 1, 2, 3, 4, 5 and 6, respectively (Table 2.1). In 2006, the *Juncus* marsh planter rows were submerged 78, 51, 26, 10, 3 and 0.4 percent of the growing season for rows 1, 2, 3, 4, 5 and 6, respectively. In 2007, the marsh planter containing half *Spartina* and half *Juncus* was submerged 100, 96, 76, 49, 24 and 7 percent of the growing season for rows 1, 2, 3, 4, 5 and 6, respectively. The marsh planter was positioned at a greater depth in 2007 in order to determine the depth beyond which *Spartina* could not survive; this had not been achieved in 2006.

LOLA. At LOLA, the difference between MSL and MHW was approximately 0.04 m and MSL is at the same elevation as NAVD88. In 2006, the *Juncus* marsh planter rows were submerged 80, 53, 28, 24, 6 and 0.7 percent of the growing season for rows 1, 2, 3, 4, 5 and 6, respectively (Table 2.1).

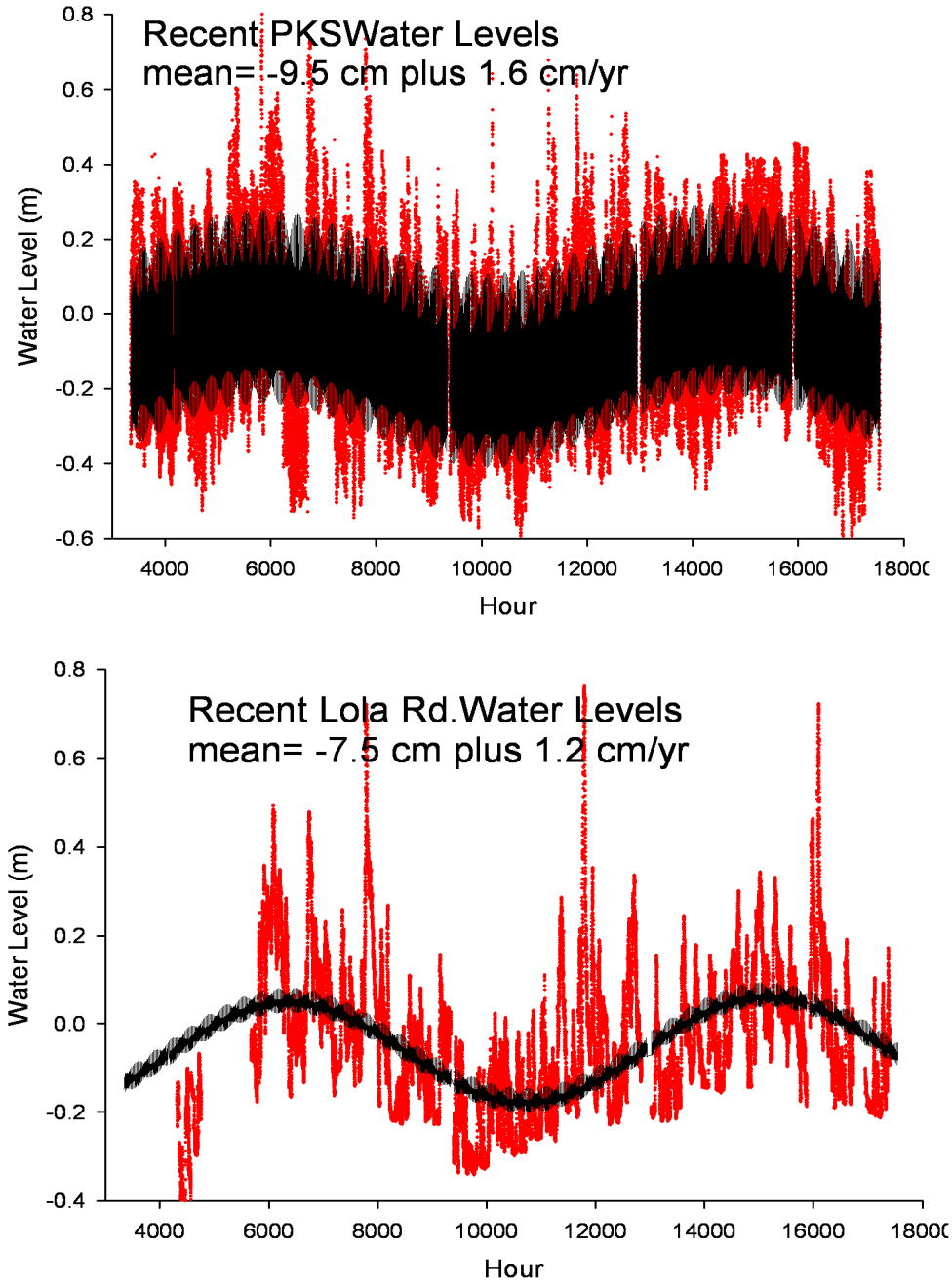


Figure 2.3. Water levels relative to NAVD88 at PKS (top) and LOLA (bottom) from mid-2006 through December 2007. Red points = observed data; black points= fitted tidal harmonics (K_1, M_2, O_1 and Sa)

Table 2.1. Elevation & percent time flooded (referenced from pot top) of all marsh planter rows

Marsh planter	row	Elevation relative to MSL (m)	Elevation relative to NAVD88 (m)	Percent time flooded (%)	Inundation (arcsine transformed value)
PKS 2006 *Spartina*	1	-0.318	-0.200	81.	1.120
	2	-0.180	-0.062	57.	0.856
	3	-0.023	0.095	28.	0.558
	4	0.099	0.217	14.	0.383
	5	0.275	0.393	3.	0.174
	6	0.422	0.540	0.5	0.071
PKS 2006 *Juncus*	1	-0.294	-0.176	78.	1.083
	2	-0.150	-0.032	51.	0.795
	3	-0.008	0.110	26.	0.535
	4	0.144	0.262	10.	0.322
	5	0.296	0.414	3.	0.174
	6	0.446	0.564	0.4	0.063
LOLA 2006 *Juncus*	1	-0.316	-0.316	80.	1.107
	2	-0.167	-0.167	53.	0.815
	3	-0.012	-0.012	28.	0.558
	4	0.142	0.142	24.	0.512
	5	0.285	0.285	6.	0.247
	6	0.452	0.452	0.7	0.084
PKS 2007 *Spartina & Juncus*	1	-0.571	-0.453	99.	1.471
	2	-0.427	-0.309	92.	1.284
	3	-0.267	-0.149	67.	0.959
	4	-0.135	-0.017	42.	0.705
	5	0.014	0.132	19.	0.451
	6	0.163	0.281	5.	0.226

Vegetation in marsh planters

Macrophytes grown in the marsh planters exhibited an unequivocal response to inundation period. Each metric exhibited a pattern of decreasing growth with increasing inundation (Table 2.2, Figure 2.4). Overall, the degree of inundation had a significant effect on: (1) *Spartina* and *Juncus* EOS and seasonal change (start-to-end of season difference) in aboveground biomass ($P< 0.001$), (2) EOS and seasonal change in aboveground density ($P< 0.001$), (3) EOS belowground biomass ($P<0.001$) and (4) EOS and seasonal change in *Juncus* demographics ($P< 0.001$) when controlled for site, year and species. These response variables did not substantially differ by inundation period at the start of each season. During each growing season, the density increase in culms (*Spartina*) and leaves (*Juncus*) was inversely proportional to inundation ($P< 0.001$), and densities actually decreased among plants inundated ≥ 92%, in most cases. The EOS *Juncus* leaf live-to-dead ratio (green: brown) decreased significantly ($P< 0.001$) with increasing inundation. The marsh planters mirrored the growth patterns of elevation-equivalent sites monitored on adjacent marsh platform.

Table 2.2. Overview of the response of *Spartina* and *Juncus* to inundation by various growth response metrics

Marsh macrophyte response to increasing inundation

	Spartina	*Juncus*
Response variable		
aboveground total EOS biomass	↘ marked ↓ ≥67% inundation	↘ marked ↓ ≥53% inundation (meteorologically-dominated regime) marked ↓ ≥42% inundation (astronomically-dominated regime)
aboveground live EOS biomass	↘	↘ marked ↓ ≥53% inundation (meteorologically-dominated regime) marked ↓ ≥42% inundation (astronomically-dominated regime)
aboveground total biomass differential	↘	↘ marked ↓ ≥42% inundation (astronomically-dominated regime)
aboveground total EOS density increase	↘ no↑ ≥ 92% inundated	↘
aboveground EOS green: brown	↔	↘ marked ↓ ≥42% inundation (astronomically-dominated regime)
belowground total EOS biomass	↘	↘

KEY:
↘ decreased linearly
↑ increase
↓ decrease
↔ no/little difference
significant relationship=**bolded**

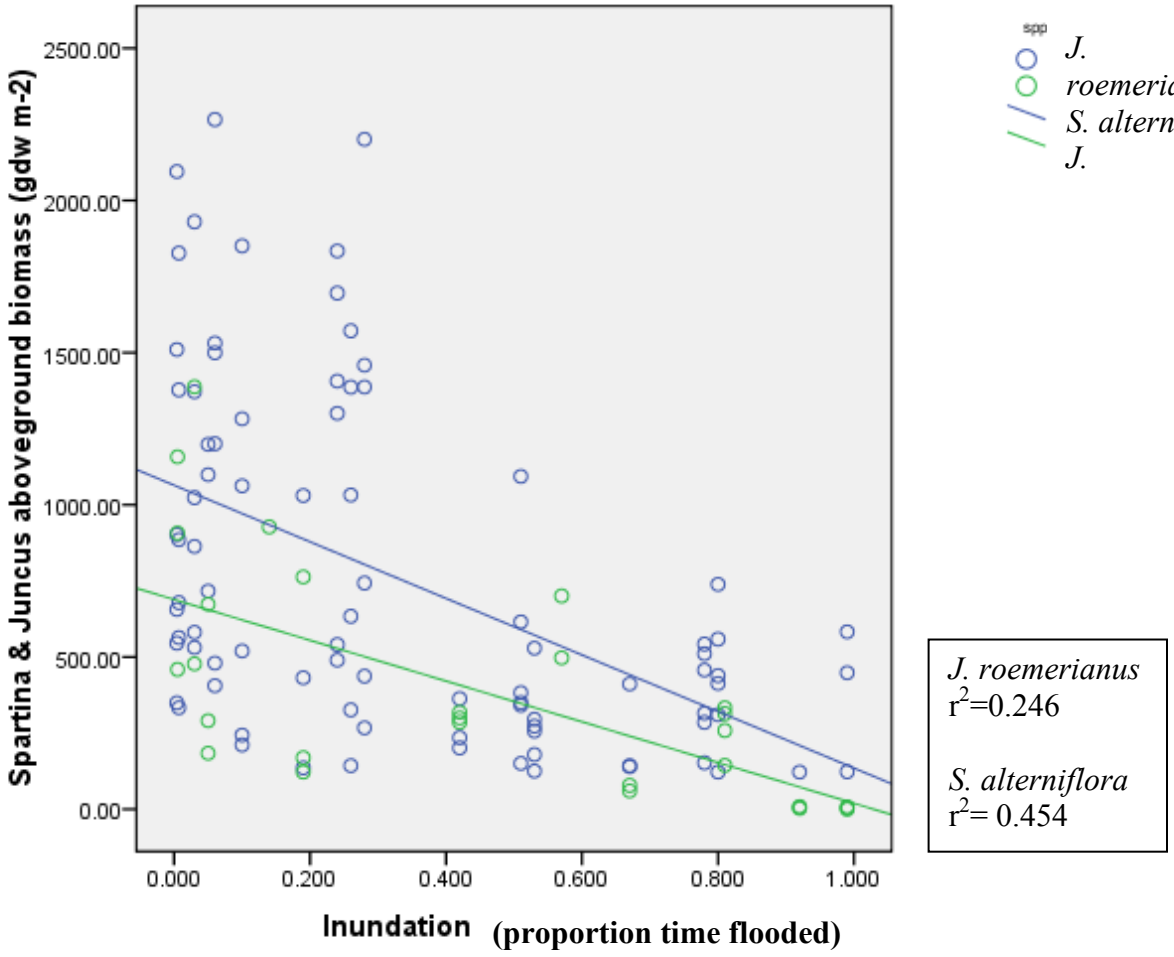


Figure 2.4. *Spartina* and *Juncus* EOS aboveground biomass grown in marsh planters to a range of inundation periods

Spartina alterniflora. The degree of inundation had a significant (*P< 0.001*) effect on the EOS and seasonal change in *Spartina* aboveground biomass (Figures 2.5 and 2.6). An increase in inundation significantly reduced the total (live and dead) *(P< 0.001*) and live *(P< 0.001)* EOS aboveground biomass of *Spartina* (Figure 2.5). Total and live EOS aboveground biomass was significantly *(P≤ 0.015)* reduced in 2007 compared to that of 2006, yet trends were similar in both years. In 2006, the total EOS *Spartina* aboveground biomass ranged from 1150.8 (SEM 138.8) to 262.5 (42.5) gdw m^{-2} at elevations inundated 0.5% and 81% of the time, respectively; in 2007, this value ranged from 382.6 (148.6) to 4.2 (2.3) gdw m^{-2} at elevations inundated 5% and 99% of the time, respectively (Table 2.3). The estimated seasonal change in biomass was also inversely related to inundation (r^2= 0.461, *P= 0.001*). Initial estimated biomass was found not to be a significant covariate in EOS biomass in either season.

During the growing seasons, *Spartina* culm density generally increased in treatments inundated ≤ 81% with the seasonal change in density showing a linear trend of decreasing density increase with increasing inundation (r^2= 0.542, *P< 0.0001*) (Figure 2.7). In addition, mean culm heights increased in all but the most-frequently inundated treatment (inundated ≥ 99%) and exhibited a parabolic relationship with inundation period (see Appendicies). During the 2007 growing season, culms were planted with a mean of 3 leaves/stem in April, this decreased to 1 leaf/stem in the lowest two elevations (≥ 92% inundation) and increased to 5 leaves/stem in the upper four elevations by September (≤ 67% inundation).

The study of demographic (proportion live (green) and dead (brown)) changes in *Spartina* over the growing seasons revealed little response to inundation period (*P= 0.630*), with the exception of culms inundated > 81% of which a greater proportion of culm length per pot was dead than live by end of growing season (Figure 2.8 (a)). Start-of-season culm demograhics were found not to be a covariate of EOS culm demographics.

The degree of inundation had a significant *(P<0.001)* effect on total EOS *Spartina* belowground biomass, illustrating a clear linear trend of decreasing biomass with increasing inundation (r^2= 0.550, *P< 0.001*) (Figure 2.9). We assume that the initial aboveground biomass was an indicator of the initial belowground biomass; initial aboveground biomass was found to not be a covariate of EOS belowground biomass (*P= 0.250*) in post-hoc tests. In 2006, total EOS *Spartina* belowground biomass ranged from 5849.8 (780.5) to 2465.1 (526.5) ash-free dry grams per square meter (afdg m^{-2}) at elevations inundated 0.5% and 81% of the time, respectively. In 2007, belowground biomass ranged from 4247.8 (438.6) to 1068.5 (296.1) afdg m^{-2} (Table 2.3) with a greater proportion of this biomass classified as dead. The more deeply submerged 2007 PKS planter exhibited reduced belowground biomass compared to that of 2006, however, this reduction was not significant (*P= 0.108*) when controlling for degree of inundation.

Table 2.3. Summary of above- and below- ground *Spartina* and *Juncus* EOS biomass showing mean (and standard error of the mean (SEM))

Marsh planter	row	Mean total aboveground biomass (SEM)	*n*	Mean total belowground biomass (SEM)	*n*
PKS 2006 *Spartina*	1	262.5 (42.5)	4	2465.1 (526.5)	6
	2	599.0 (101.8)	2	3215.6 (278.7)	6
	3	-	0	3719.9 (509.2)	6
	4	927.3	1	4379.0 (704.5)	6
	5	932.5 (455.1)	2	5829.0 (653.6)	5
	6	1150.8 (138.8)	3	5849.8 (780.5)	6
PKS 2006 *Juncus*	1	377.2 (61.7)	6	4874.6 (881.4)	6
	2	489.0 (135.2)	6	4321.1 (1095.9)	6
	3	848.9 (235.5)	6	3948.3 (935.2)	6
	4	861.8 (265.7)	6	4294.5 (442.7)	6
	5	1050.2 (216.2)	6	5462.8 (784.0)	6
	6	1009.7 (271.8)	6	7753.1 (762.2)	6
LOLA 2006 *Juncus*	1	430.3 (85.9)	6	3312.7 (295.1)	6
	2	276.5 (56.8)	6	3831.2 (434.6)	6
	3	1082.4 (299.0)	6	4953.9 (342.5)	6
	4	1211.2 (233.8)	6	5807.0 (504.7)	6
	5	1230.6 (287.5)	6	5538.7 (1008.9)	6
	6	944.4 (228.0)	6	5819.0 (341.2)	6
PKS 2007 *Spartina*	1	4.2 (2.3)	3	1448.5 (374.0)	3
	2	5.5 (1.6)	3	1068.5 (296.1)	3
	3	69.0 (9.1)	2	2545.6 (389.0)	3
	4	301.3 (9.6)	3	4247.8 (438.6)	3
	5	351.3 (206.2)	3	3289.7 (461.4)	3
	6	382.6 (148.6)	3	4035.4 (781.2)	3
PKS 2007 *Juncus*	1	384.8 (136.5)	3	2322.7 (444.5)	3
	2	122.1	1	3658.2	1
	3	231.4 (90.0)	3	1693.3 (776.7)	3
	4	266.4 (49.3)	3	3320.1 (1082.1)	3
	5	532.8 (263.2)	3	2112.5 (277.4)	3
	6	1004.7 (146.9)	3	2434.0 (387.1)	3

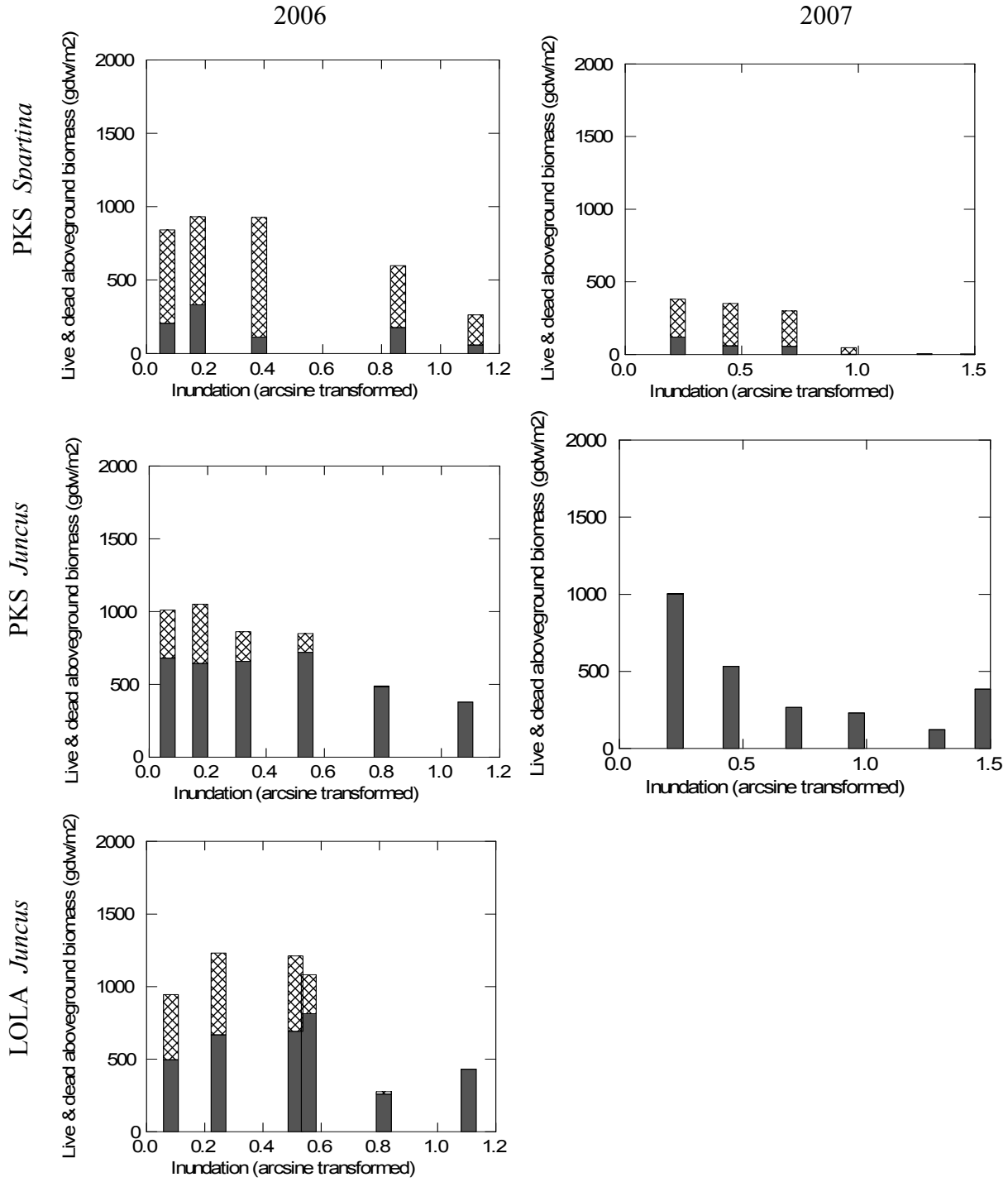
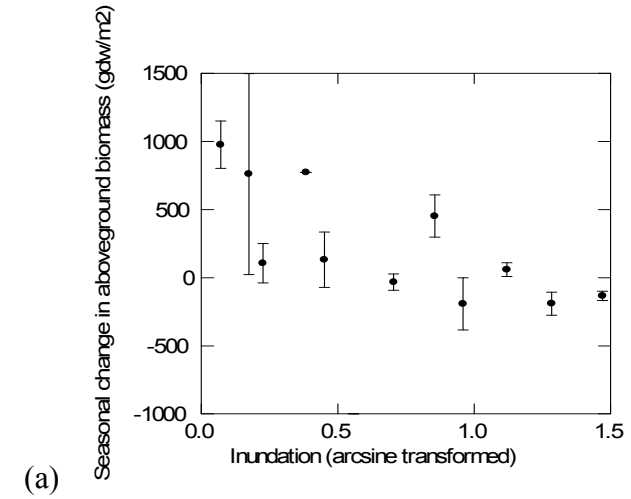
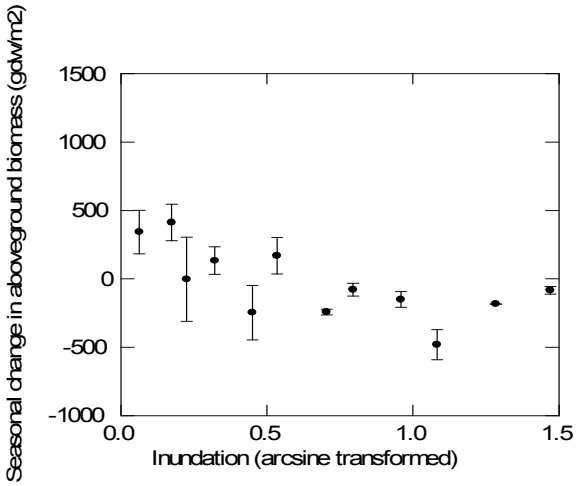


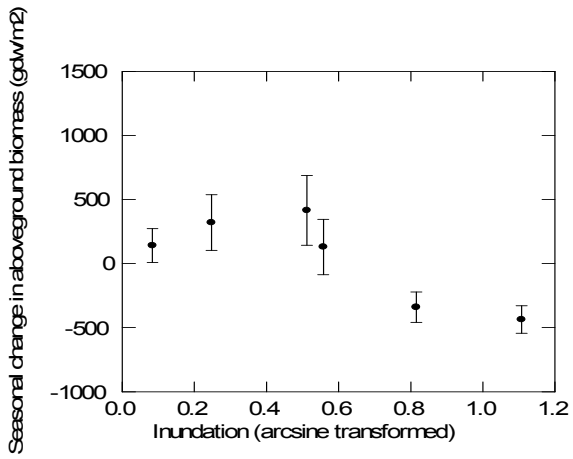
Figure 2.5. Live (checkered) and dead (solid gray) end-of-season aboveground biomass of *Spartina* and *Juncus* planters at PKS and LOLA



(a)

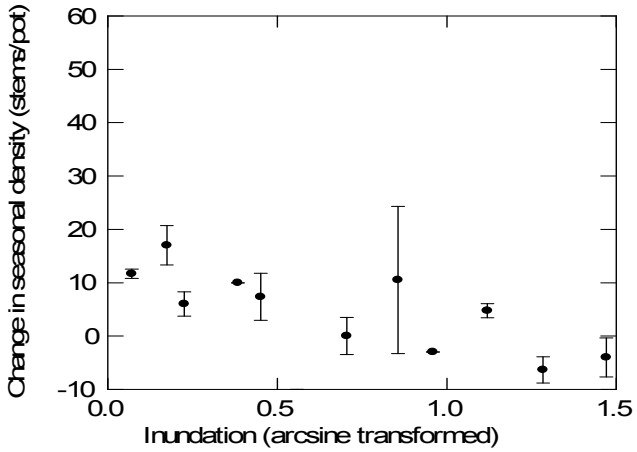


(b)

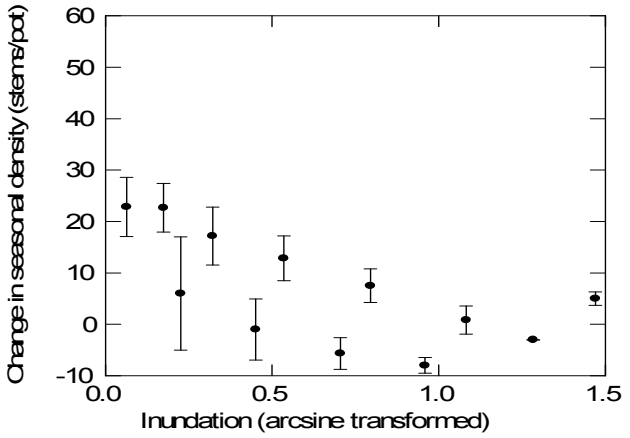


(c)

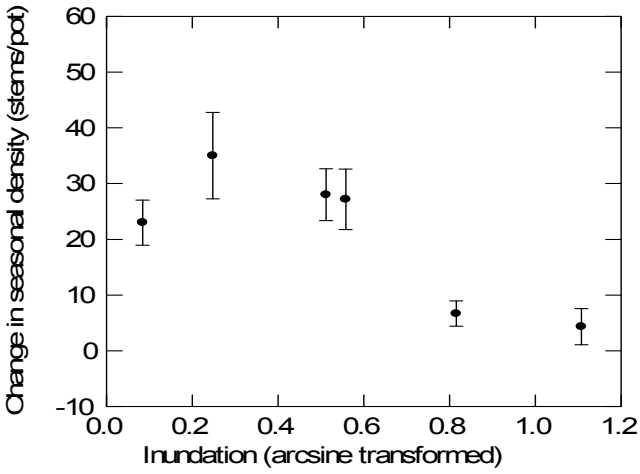
Figure 2.6. Seasonal change in aboveground biomass of (a) PKS *Spartina*, (b) PKS *Juncus* and (c) LOLA *Juncus*



(a)



(b)



(c)

Figure 2.7. Seasonal change in the density of PKS *Spartina* (a), PKS *Juncus* (b) and LOLA *Juncus* (c)

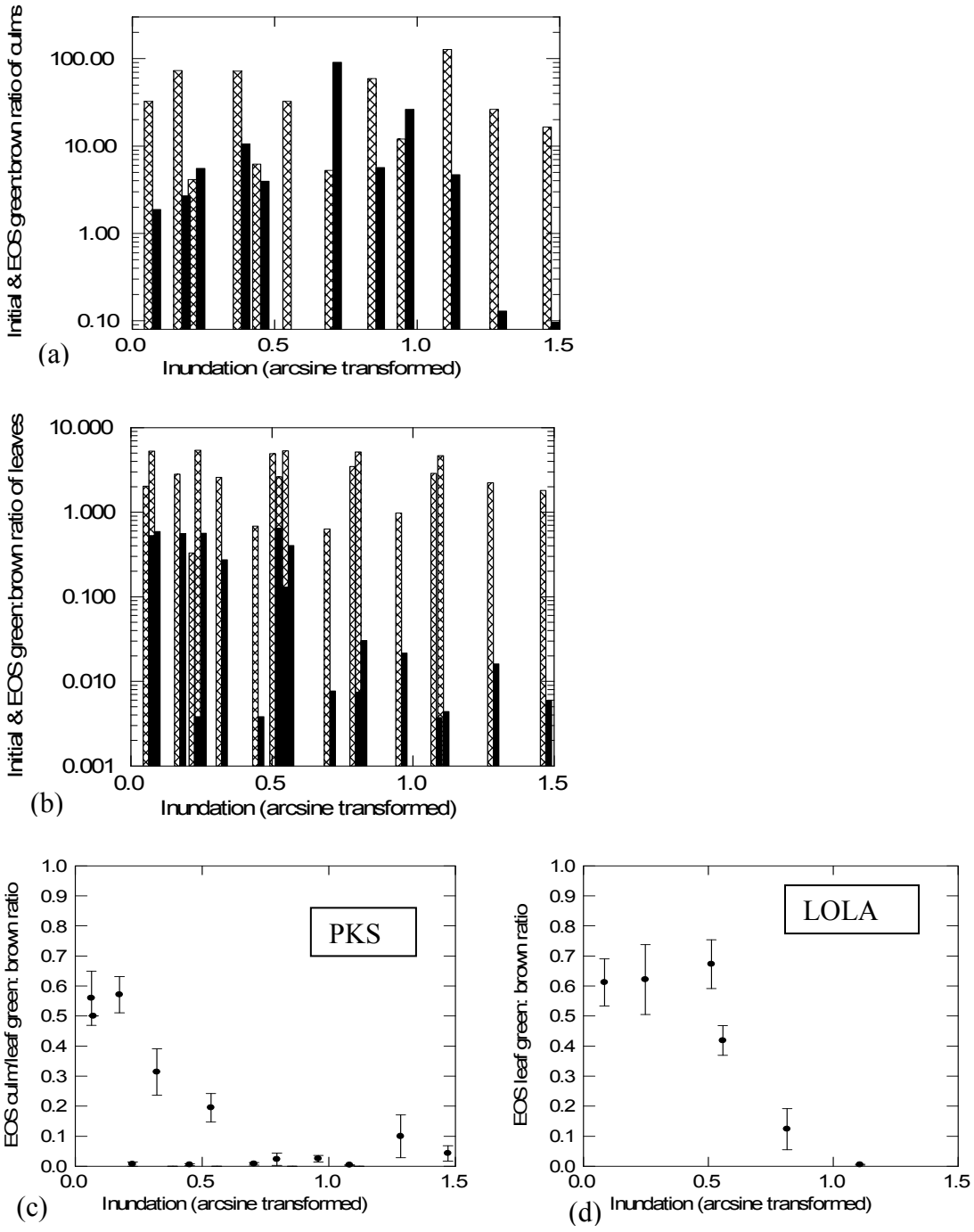


Figure 2.8. Initial (checkered bars) & EOS (black bars) culm (*Spartina*) and leaf (*Juncus*) demographics of of (a) *Spartina* and (b) *Juncus* (Note: Y-axis log scales differ by species) and EOS *Juncus* green:brown leaf ratio at (c) PKS and (d) LOLA

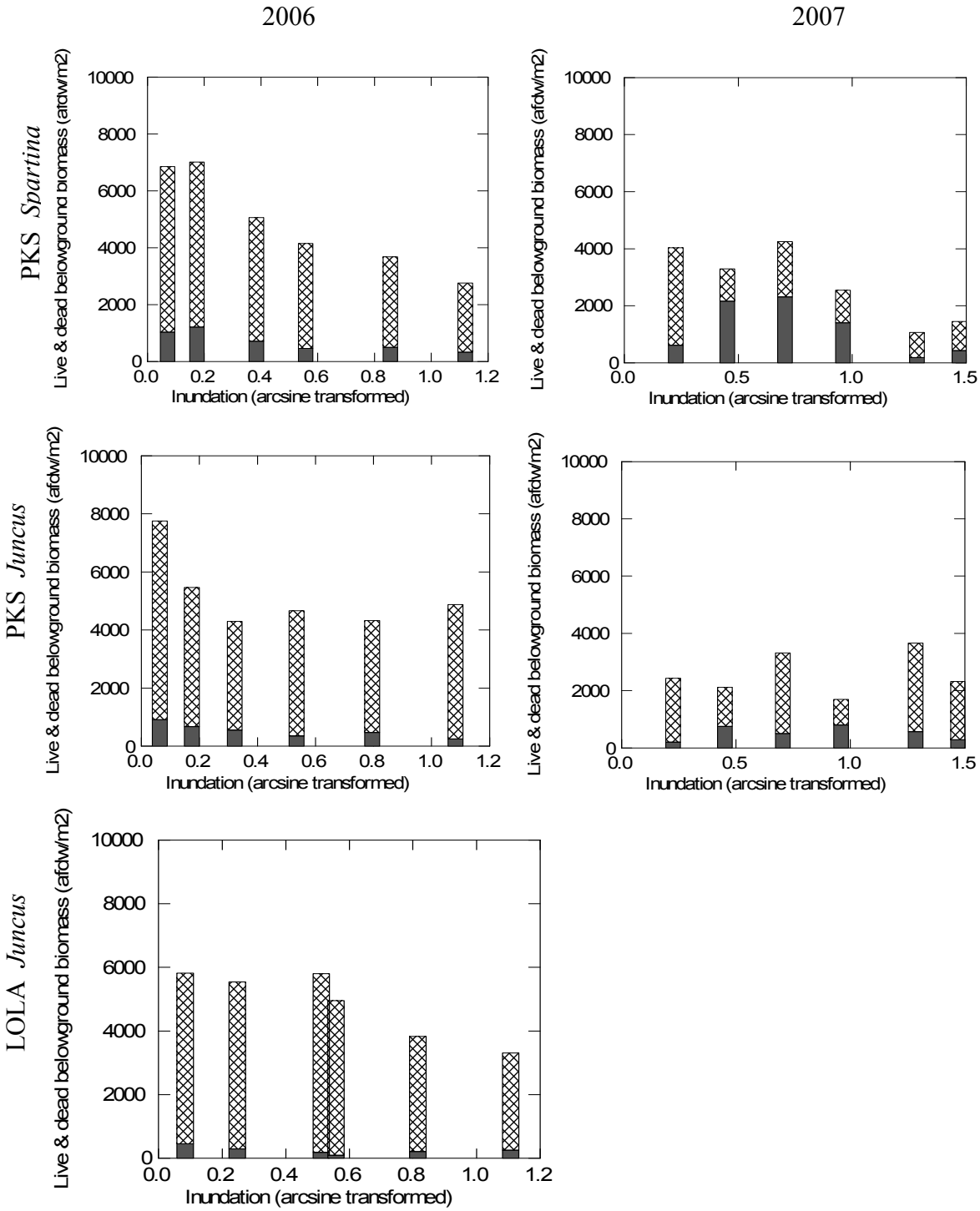


Figure 2.9. Live (checkered) and dead (solid gray) end-of-season belowground biomass of *Spartina* and *Juncus* planters at PKS and LOLA

Juncus roemerianus. The degree of inundation had a significant (*P< 0.001*) effect on the total and live EOS and seasonal change in the aboveground biomass of *Juncus* (Figures R3 and 3a). Total EOS aboveground *Juncus* biomass did not differ significantly between years *(P= 0.183)* or sites (*P= 0.211*) and the overall response to inundation was similar. End-of-season live biomass was significantly *(P= 0.001*) reduced in 2007 when compared to that of 2006 at PKS (no planter at LOLA in 2007). The seasonal change in biomass was inversely related to inundation (r^2= 0.288, *P< 0.0001*). Estimated initial biomass was found not to be a significant covariate in EOS aboveground biomass in 2006 but was found to be a covariate in 2007 (*P= 0.04*) although estimated initial biomass did not differ significantly among treatments in 2007 (*P= 0.117*). The seasonal change in *Juncus* aboveground biomass showed a marked reduction when inundated ≥ 28% of the time, especially at the irregularly-flooded site (LOLA) (Figures R3 and R3a). These data fit a polynomial model (r^2= 0.304, *P= 0.0001*) better than a linear model (r^2= 0.292, *P= 0.0001*), suggesting a threshold response to inundation.

At PKS, little live *Juncus* aboveground biomass remained in treatments with inundation times exceeding 50%. At PKS in 2006, total EOS *Juncus* aboveground biomass ranged from 377.2 (61.7) to 1050.2 (216.2) gdw m^{-2} at elevations inundated 51% and 0.4% of the time, respectively (Table 2.3). Here, virtually no live aboveground material remained at treatments receiving ≥ 51% inundation, yet there was no significant difference *(P = 0.16)* in total biomass by inundation period due to high variability in this measure (Figure 2.5). In 2007 at PKS, total EOS *Juncus* aboveground biomass ranged from 122.1 to 1004.7 (146.9) gdw m^{-2} at elevations inundated 92% and 5% of the time,

respectively (Table 2.3). Only one pot of three in the treatment receiving least inundation (0.4%) contained live *Juncus* in September 2007. At LOLA in 2006, total EOS *Juncus* aboveground biomass ranged from 276.5 (56.8) to 1230.6 (287.5) gdw m^{-2} at elevations inundated 53% and 6% of the time, respectively, showing a trend of decreasing biomass with increasing inundation with a marked decrease at elevations inundated ≥ 28% and little live material present at elevations inundated ≥53% (Table 2.3).

Significant ($P \leq 0.05$) increases in *Juncus* leaf density occurred at inundation periods ≤ 53%, and EOS density showed a linear trend of less density with increasing inundation ($r^2 = 0.215$, $P < 0.0001$) (Figure 2.7). The seasonal change in *Juncus* density differed significantly ($P < 0.0001$) by site as well, with higher densities generally observed at LOLA (discussed in detail below see *Inundation regime effects on Juncus*). Estimated mean *Juncus* leaf height (total pot leaf length divided by density) decreased through the 2006 and 2007 growing seasons in all treatments, associated with the general increase in leaf densities; however, the mean leaf height response to inundation differed significantly between sites ($P = 0.001$). At PKS, the effect of inundation on mean leaf height was not significant ($P = 0.303$). At LOLA, the effect of inundation on the seasonal change in leaf height was significant ($P < 0.001$), showing a smaller increase in leaf height with increased inundation.

An analysis of *Juncus* demographics showed that inundation had a significant ($P < 0.001$) effect on the EOS live-to-dead ratio (green: brown) of *Juncus* leaves and that this variable differed significantly by site ($P < 0.001$). The initial leaf green: brown was found not to be a covariate of this EOS ratio. Both sites showed the same EOS trend of

decreasing green: brown with increasing inundation, yet *Juncus* leaves at LOLA had a higher proportion of green than those at PKS (Figure 2.8). A survey of demographics at PKS in July 2006 showed that the increase in density was similar (*P= 0.91*) among elevations with a mean March-July increase of 11.5 (1.1) leaves/pot; however, all elevations decreased significantly (*P≤ 0.002*) in the green-leaf height between March and July. Thereafter, the green-leaf height changed little among treatments, except, at the elevation inundated 3% where the green-leaf height was greatest (*P= 0.05*). End-of-season leaf green: brown were dramatically reduced at elevations inundated ≥ 53% at LOLA and at elevations inundated ≥ 42% at PKS (Figure 2.8 (c and d)).

Inundation time had an overall negative linear effect (P< 0.0001) on total EOS *Juncus* belowground biomass, and no differences were found in this response between sites (*P= 0.288*) (Figure 2.9). At PKS, the EOS belowground biomass response to inundation differed significantly (*P=0.001*) by year, with 2006 EOS belowground biomass illustrating the predominant trend decreasing biomass with increasing inundation (*P=0.060*) and the more deeply submerged 2007 PKS planter exhibiting reduced belowground biomass compared to that of 2006 and showing no clear trend (*P=0.961*) (Figure 2.9). At PKS in 2006, total EOS *Juncus* belowground biomass ranged from 3948.3 (935.2) to 7753.1 (762.2) afdg m^{-2} at elevations inundated 26% and 0.4% of the time, respectively (Table 2.3). In 2007, total EOS *Juncus* belowground biomass ranged from 1693.3 (776.7) to 3658.2 afdg m^{-2} at elevations inundated 67% and 92% of the time, respectively (Table 2.3). It is likely that little, if any, belowground growth occurred in the 2007 PKS planter. At LOLA in 2006, total EOS *Juncus* belowground biomass ranged

from 3312.7 (295.1) to 5819.0 (341.2) afdg m^{-2} at elevations inundated 80% and 0.7% of the time, respectively. Thus, showing a trend ($P< 0.0001$) of decreasing biomass with increasing inundation with a marked decrease at elevations inundated ≥ 28% and little live material present at elevations inundated ≥53% (Figure 2.5). As with *Spartina*, initial *Juncus* aboveground biomass was used as an indicator to approximate the initial belowground biomass; initial aboveground biomass was found to be a covariate of EOS belowground biomass ($P= 0.024$) when grouped, but not significant when considered by marsh planter ($P\leq 0.112$).

Juncus response by inundation regime

The response of *Juncus* to inundation period was compared by inundation regime. We observed only modest differences in *Juncus* response between astronomically-dominated (PKS) and meteorologically-dominated (LOLA) inundation regimes. Like rows of *Juncus* grown in planters at PKS and LOLA experienced inundation for similar periods of time allowing direct pairwise comparisons by planter row. In addition, we compared LOLA row 4 (24% inundation) with PKS row 3 (26% inundation), as these treatments were also analogous (Table 2.1).

Overall, response metrics revealed that *Juncus* was likely more stressed when grown in planters within an astronomically-dominated than within a meteorologically-dominated inundation regime. A GLM ANOVA showed the total EOS aboveground biomass of *Juncus* experiencing similar inundation periods differed little with inundation regime ($P\geq 0.178$) (Table 2.3). Site was a significant factor explaining differences in EOS live aboveground *Juncus* biomass ($P=0.035$) and seasonal density increase ($P=$

0.005), along with inundation period (*P < 0.0001*); no interaction was indicated for live biomass (P= 0.327) or density (*P= 0.253*) (Figures 2.5 and 2.7). Two-sample t-tests were used to compare *Juncus* growth response to inundation regime at analogous inundation periods. The seasonal change in total aboveground biomass was greater (*P= 0.047*) at LOLA than at PKS, when inundated 53% and 51%, respectively. The difference in EOS live aboveground biomass differed significantly (*P=0.0132*) when comparing inundated 26 % at PKS and 24% at LOLA. The seasonal change in *Juncus* density was greater at LOLA when compared to PKS when inundated 24% and 26% (*P= 0.025*) and 28% and 26% (*P= 0.045*). A proxy for *Juncus* leaf health, leaf green: brown were generally higher at LOLA indicating that *Juncus* at LOLA experienced less stress than *Juncus* at PKS. This parameter was significantly higher at LOLA when compared to PKS for *Juncus* inundated 24 and 10% (*P=0.005*), 28 and 26% (*P= 0.005*) and 24 and 26% (*P= 0.0002*). All of the significant differences observed in aboveground material occurred at inundation periods experienced by *Juncus* on the marsh platform at each site. A GLM ANOVA showed that site did not explain differences in EOS belowground biomass of *Juncus* (P= *0.775*). Two-sample t-tests showed that EOS belowground biomass was greater at LOLA than at PKS when inundated 24% and 10% (*P= 0.048*) and 0.7% and 0.4%, (*P= 0.043*).

Planter-platform comparisons

The growth response of vegetation cultivated in the marsh planters reflected that of the adjacent marsh platform at analogous inundation periods. The total EOS aboveground biomass did not differ significantly between planter and platform within

respective site and species groups (Table 2.4 and Figure 2.10). However, this response variable did show more variability in the marsh mesocosms than on the marsh platform. There was only one point at which the total EOS aboveground biomass grown in the planter was significantly lower than the platform plot experiencing equivalent inundation times. This difference occurred in the 81% inundation treatments of *Spartina* (PKS only) where the EOS aboveground biomass in this platform plot was both greater (*P=0.003*) than that of the planter.

Table 2.4. Comparison of marsh planter and marsh platform end-of-season aboveground biomass

Site / species	planter row	Elevation relative to MSL (m)	Mean EOS aboveground biomass (gdw m^{-2})				P value
			Marsh planter mean (SEM)	*ŋ*	Marsh platform mean (SEM)	*ŋ*	
PKS *Spartina*	1	-0.086	**262.5** (42.5)	4	**758.21** (97.70)	5	**0.003**
	2	0.056	599.00 (101.8)	2	403.48 (76.96)	5	0.220
	3	0.213	-	0	617.65 (11.55)	2	-
	4	0.335	927.3	1	435.97 (97.46)	6	-
	5	0.511	932.5 (455.1)	2			
	6	0.658	1150.8 (138.8)	3			
PKS *Juncus*	1	-0.058	377.2 (61.7)	6			
	2	0.086	489.0 (135.2)	6	-		-
	3	0.228	848.9 (235.5)	6	987.07 (205.65)	6	0.400
	4	0.380	861.8 (265.7)	6	484.00 (77.55)	2	0.470
	5	0.532	1050.2 (216.2)	6			
	6	0.682	1009.7 (271.8)	6			
LOLA *Juncus*	1	-0.316	430.3 (85.9)	6			
	2	-0.167	276.5 (56.8)	6			
	3	-0.012	1082.4 (299.0)	6			
	4	0.142	1211.19 (233.77)	6	993.47 (64.7)	6	0.225
	5	0.285	1230.6 (287.5)	6			
	6	0.452	944.4 (228.0)	6			

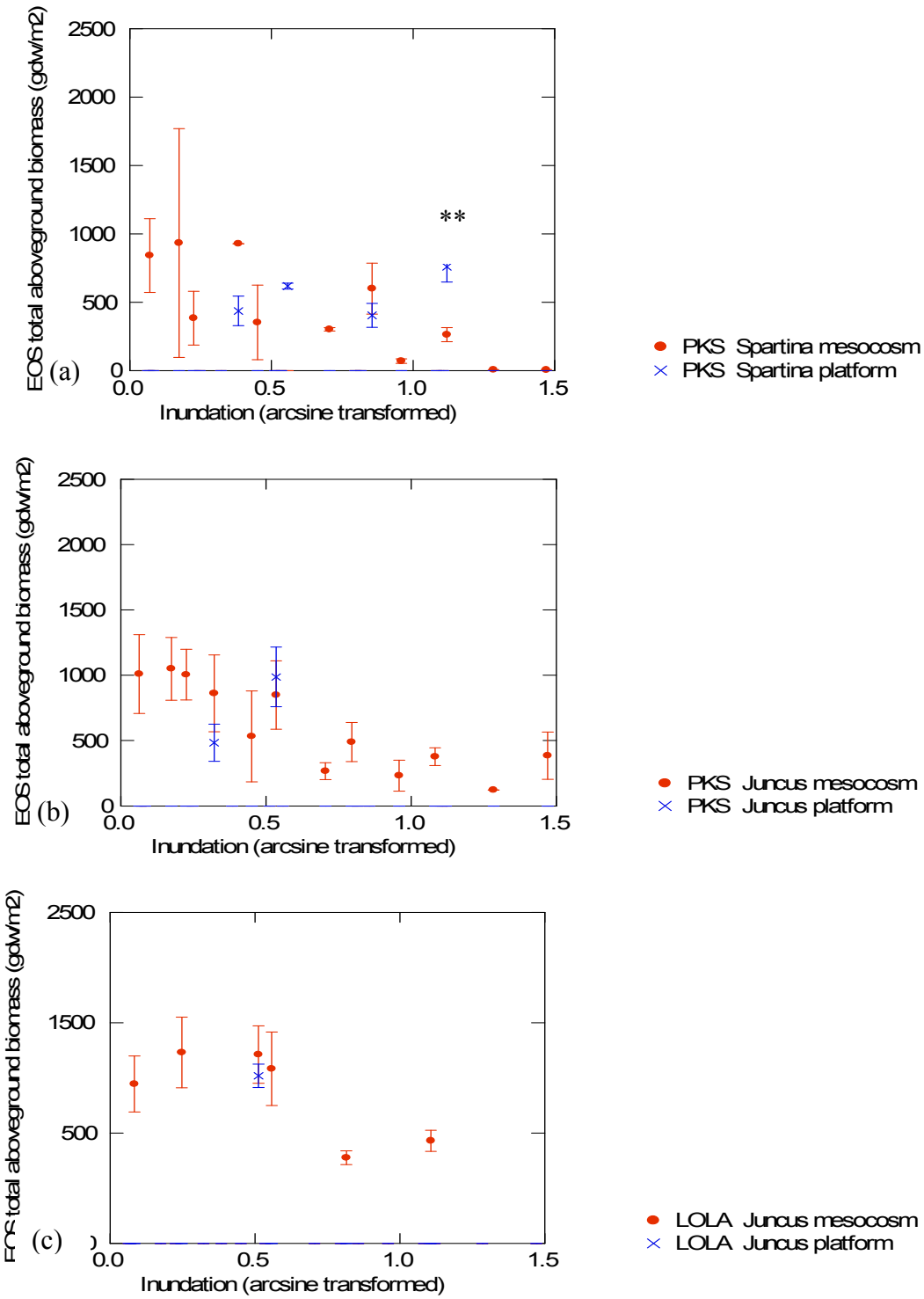


Figure 2.10. EOS aboveground total biomass comparisons of (a) *Spartina* at PKS and (b) *Juncus* at PKS and (c) *Juncus* at LOLA in marsh planters (red) and adjacent marsh platform (blue) ** $P < 0.001$

DISCUSSION

We examined the growth response of two dominant marsh macrophytes over a range of inundation periods in an effort to understand better how coastal marshes will respond to the increased flooding inherent from sea-level rise. Marsh vegetation is likely key to accretion processes, whereby increased aboveground density and biomass baffles floodwaters, thus potentially increasing the degree of sedimentation, and increased belowground biomass contributes directly to the elevation of marsh substrate (Cahoon 1998, Morris et al. 2002). We utilized multi-level marsh planters to alter the elevation at which *Spartina alterniflora* and *Juncus roemerianus* grew for two growing seasons, thus exposing each species to a range of inundation periods (extending the range experienced by macrophytes beyond that of the adjacent marsh platform). Additionally, for *Juncus*, we compared the response to inundation period by inundation regime (regular, astronomically-dominated and irregular, meteorologically-dominated flooding patterns). We measured an array of response metrics in an attempt to fully resolve macrophyte response to inundation. Significant trends of decreasing production with increasing inundation were observed across most response variables measured. The production patterns of *Spartina* and *Juncus* to inundation period were similar (Figures 2.5 and 2.6); though, *Juncus* appeared to experience greater stress at the astronomically-dominated inundation site as compared to the meteorologically-dominated inundation site (Figure 2.8 (c and d)). We observed essentially no seasonal increase in *Spartina* biomass at elevations inundated $\geq$ 67 % (PKS only) and no seasonal increase in *Juncus* biomass at

elevations inundated ≥ 42 % and ≥ 53 % at PKS and LOLA, respectively (Figure 2.6). In addition, *Spartina* culms and *Juncus* leaves were largely dead at the end of the growing season at elevations inundated ≥ 92 % and ≥ 42 to 53 %, respectively (Figure 2.8). Throughout each growing season, culm and leaf densities increased at all elevations, however, this increase was negatively correlated with inundation (Figure 2.7).

Aboveground biomass

In the NC planters, we found that peak *Spartina* aboveground production occurred between 0.10 to 0.42 m above MSL, corresponding to inundation periods of 14 to 0.5% (Figure 2.11). In similarly designed planter studies in SC, peak *Spartina* production occurred between 0.3 to 0.6 m above MSL, inundation periods were not measured (Morris and Sundberg 2008). Peak *Juncus* aboveground production occurred at -0.01 to 0.45 m MSL in the astronomically-dominated site and -0.01 to 0.29 m MSL at the meteorologically-dominated site, these elevations corresponded with inundation periods of 26 to 0.4% and 28 to 6% at PKS and LOLA, respectively. Using MSL as a point of reference may adequately consider site specific differences in tidal range and other hydrologic factors that influence edaphic conditions (i.e., hydraulic head, aquatic exchange rates) as we discuss below. We anticipate that our findings of peak macrophyte production corresponding to inundation period, and perhaps to elevation relative to MSL (approximate range 0 – 0.4 m MSL), may be true for coastal marshes more broadly. We found the relationship between elevation and inundation period to be generally linear, yet, this relationship differs by geographic location due to the influence of astronomical and meteorological effects on water level.

Our results showed a trend of macrophyte production being inversely related to inundation period. This differed from previous such studies and challenged us to define the relationship between production and inundation. In similarly-designed studies using multi-level planters to manipulate macrophyte inundation, Morris and Sundberg (2008, pers. comm.) observed a trend of increasing *S. alterniflora* biomass with increasing inundation at a site that experienced a 1.4-meter mean range in tide at North Inlet, South Carolina. Corroborating these findings are the observations of *S. alterniflora* production being strongly and positively correlated to changes in local MSL and/or rainfall at the same North Inlet site (Morris and Haskins 1990). This increase in biomass appears to be the well established relationship typically associated with an increase in the height, rather than density of *Spartina* (Gallagher 1974, Nixon and Oviatt 1972, Broome et al. 1975, Haines and Dunn 1976). Several investigations (Turner 1976, Pomeroy et al. 1981, King et al. 1982) note the presence of tall-form *S. alterniflora* near marsh creek and estuarine edges. Although relatively little research has focused on the ecology of *Juncus*-dominated marshes, several investigations have shown *Juncus* to occur over a wide range of physical and chemical variables (Kruczynski et al. 1978, Eleuterius 1976, Christian et al. 1990, Woerner and Hackney 1997, Brinson and Christian 1999, Touchette 2006). *Juncus* biomass, density (Kruczynski et al. 1978, Christian et al. 1990, Touchette 2006) and height (Kruczynski et al. 1978) have been found to decrease with distance from estuarine edge or with increased sand content of substrate (Woerner and Hackney 1997). The standing crop of growing leaves (Christian et al. 1990) and leaf height (Woerner and Hackney 1997) of *Juncus* have been negatively correlated with elevation and salinity.

Hook (1991) found that *Juncus* biomass was limited by inundation and salinity within the estuarine edge zone (~200 m from edge) and by nitrogen in the marsh interior (~ 1.6 km from edge). Voss (2006) found that *Juncus* dominance was inversely related to elevation where thin-layers of dredged spoil were added to marsh surface. Hence, there is a preponderance of evidence suggesting that macrophyte production is positively correlated with inundation at least up to some undetermined threshold.

In marsh habitats, macrophyte populations experience two divergent gradients of aerobic-to-anaerobic edaphic conditions with estuarine inundation being the source of a stress-subsidy-stress phenomenon. For marsh macrophytes (notably *Spartina*), edge habitat offers more favorable edaphic conditions than more inland areas due to the increased oxygenation and the greater exchange rate of water in soils within the edge environ (i.e., oxygenated pore space allowing aerobic root respiration, low sulfide levels and the consequential favorable ammonium kinetics (low K_m and high V_{max}) that facilitate ammonium uptake) relative to interior zones (Mendelssohn et al. 1981, Morris and Dacey 1984, Mendelssohn and Morris 2000). From the edge zone (which receives greatest tidal subsidy), a landward gradient occurs toward an anoxic zone that receives infrequent inundation and becomes hydraulically isolated, where the estuarine hydraulic head disallows soil drainage, redox potential decreases and salinity may accumulate (Odum et al. 1983, Bertness and Hacker 1994, Pezeshki 2001). The opposing seaward gradient receives increasing periods of inundation where respiratory and sulfide toxins are flushed. Along this continuum, soils become increasingly saturated and wave-stress increases. Along this seaward gradient, the lack of hydraulic isolation may permit

Spartina to respond to anoxic conditions by increasing aboveground biomass as a mechanism to oxidize the rhizosphere (Howes et al. 1986). However, under intense anoxic conditions, with near constant flooding (saturation), *Spartina* is unable to maintain aerobic respiration, resulting in a net reduction in productivity (Mendelssohn et al. 1981).

Visual observations of edge-zone marsh habitat at our NC research sites revealed that greater inundation elicited a growth response in *S. alterniflora*. At our astronomically-dominated inundation site (PKS) we observed an overall greater degree of standing crop production within the estuarine edge zone relative to interior zones, as expected. At PKS, the marsh habitat occupies lower elevations within a dune-and-swale geomorphic setting, low marsh ramps gradually to high marsh with few tidal creeks. Here, we observed the greatest *Spartina* production (taller *Spartina*) within sections of marsh platform edge that had slumped into the estuary due to erosive undercutting and thus received the greatest inundation. At our meteorologically-dominated inundation site (LOLA) we observed no gradient of *Spartina* production with proximity to estuarine edge, as this marsh is typically inundated uniformly. The LOLA site is a true "platform" marsh with a rather uniform elevation and about a 1-m drop to the adjacent estuarine bottom, seaward of the platform edge. Collectively, our visual observations of marsh habitat at our research sites support the commonly held hypothesis that *S. alterniflora* production is positively correlated to inundation up to a threshold, yet our results in marsh planters contrast with these observations. Hence, there exists a seeming conundrum – for which we extend the Morris et al. (2002) hypothesis. *Spartina alterniflora* responds to increased inundation by increasing aboveground biomass (Morris

et al. 2002), as long as the rhizosphere is sufficiently oxygenated (as per Mendelssohn and Seneca 1980, Mendelssohn et al. 1981, Mendelssohn and McKee 1983, Mendelssohn and Morris 2000). Soil redox potential (Eh) is positively correlated with nutrient availability and *Spartina* aboveground production (Linthurst 1979, King et al. 1982, Howes et al. 1986). *Spartina alterniflora* oxidizes the sediments in which it grows through metabolic processes and diffusion, and culm heights are positively correlated with sediment oxidation status (Howes et al. 1981). There appears to be a feedback loop between well-oxidized soils yielding greater production (Linthurst 1979, King et al 1982) and an effect of increased production increasing sediment oxidation status (Howes et al. 1981, Howes et al. 1986). We postulate that shoot elongation is a stress response to increased inundation (as per Howes et al. 1981, Laan and Blom 1990, Blom and Voesenek 1996, Grimoldi et al. 1999, Insauti et al. 2001) and that by increasing aboveground biomass (particularly height), *Spartina* provides a mechanism by which to oxygenate the root zone (Anderson 1974, Howes et al. 1986, Howes and Teal 1994). If successful in adequately maintaining an aerobic rhizosphere, *Spartina* can respire aerobically and thus yield positive net productivity (as per Howes et al. 1986). There is likely a transition, as inundation period increases, where aerobic respiration transitions to dominance by anaerobic respiration. In addition, there exists some soil saturation threshold at which anaerobic respiration can no longer maintain ample cellular metabolism and vegetation eventually dies due to anoxic conditions (Ricard et al. 2006). Hence, as inundation period is prolonged and prevents recurring aerobic conditions,

Spartina dies and the border between marsh and unvegetated benthic habitat is defined. We found the inundation threshold for *Spartina* at PKS to be approximately 67 %.

These findings of marsh macrophyte response to inundation can be considered in terms of Odum et al. (1979) tidal subsidy-stress hypothesis. Inundation pulses can provide a subsidy to the macrophyte community by flushing soils (importing nutrients and exporting toxins), yet prolonged inundation (e.g., ponding without pulsing) serves as a stressor (producing an anaerobic environment) (Mendelssohn and Seneca 1980). We posit that it is the duration of inundation and resulting edaphic conditions to which macrophytes respond in a unimodal subsidy-stress curve as presented by Odum et al. (1979, Figure 2.11). Inundation period for a given elevation varies with inundation regime and is site specific; this is key in determining the oxic condition and exchange rates within marsh substrates. On daily time-scales, the pulsing of astronomical tides may serve to aerate intertidal habitats. This fact may explain why McKee and Patrick (1988) reported that *S. alterniflora* occurred over a greater range of elevation at sites where a greater range in tide was present. In addition, the pulsing paradigm has been proposed to explain why Steever et al. (1976) observed a strong positive correlation between *Spartina* productivity and tidal range, suggesting that tidal energy was transformed by macrophyte mediation into chemical energy in the form of primary production (Odum et al. 1995). Howes et al. (1986) suggest that increased porewater drainage may serve as a mechanism for the proposed tidal subsidy of *Spartina* production (Steever et al. 1976, Odum et al. 1979). It is likely that ecosystems within meteorologically-dominated inundation regimes also have a pulse (Voss 2006), albeit on

longer (at least seasonal) time-scales. Interestingly, we found *Juncus* production to be similar at analogous inundation periods at each of our research sites, under two differing inundation regimes (Tables 2.1 and 2.3). Figure 2.11 illustrates the relationship between macrophyte production and inundation and processes that influence this relationship. Figure 2.12 illustrates above- and below- ground biomass data from marsh mesocosm studies within this conceptual framework.

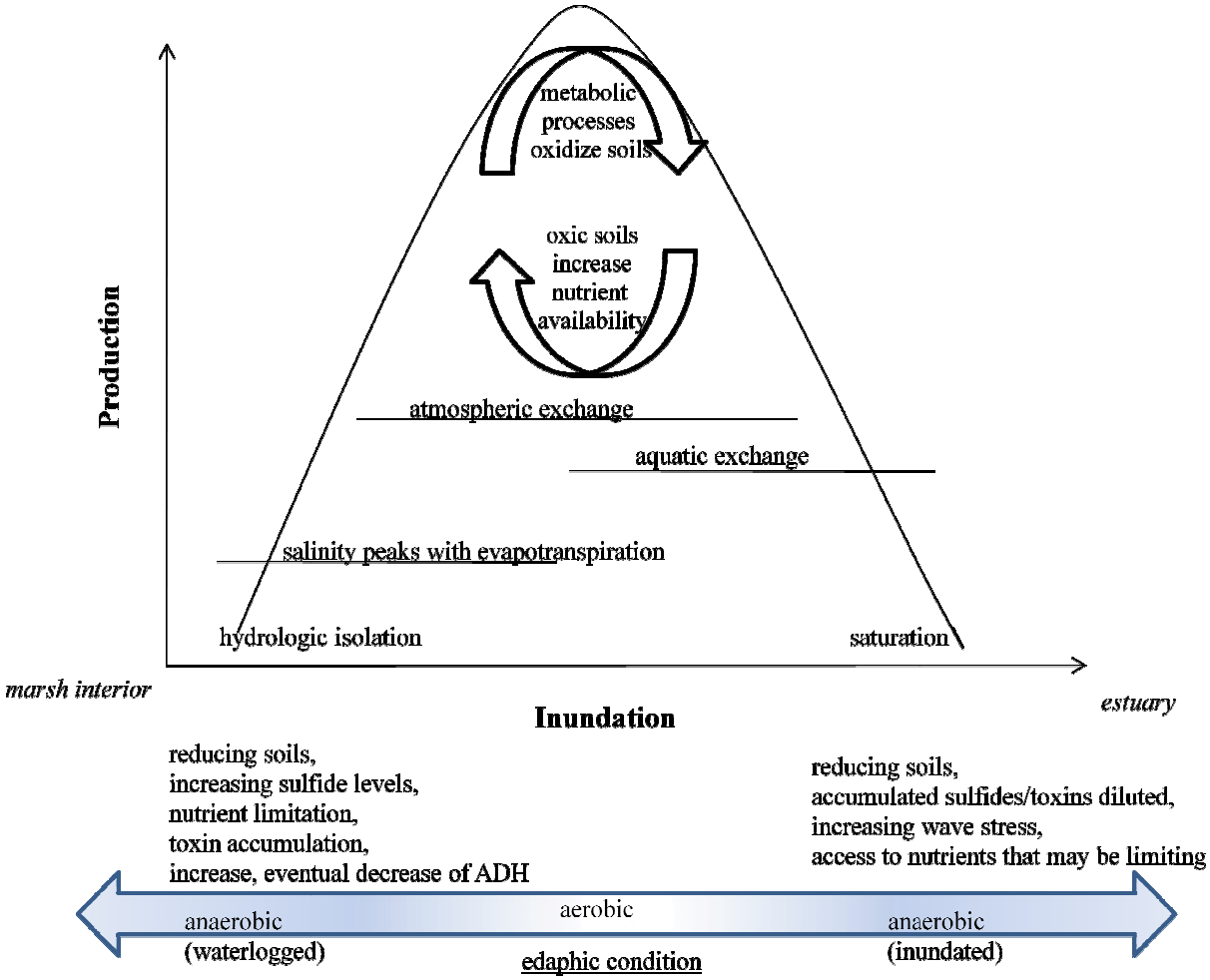


Figure. 2.11. Conceptual diagram of the relationship between marsh macrophyte production and inundation and associated processes. This relationship can be described as inundation being a stress-subsidy-stress to macrophyte production along a shore-normal marsh transect (as per Odum et al. 1979)

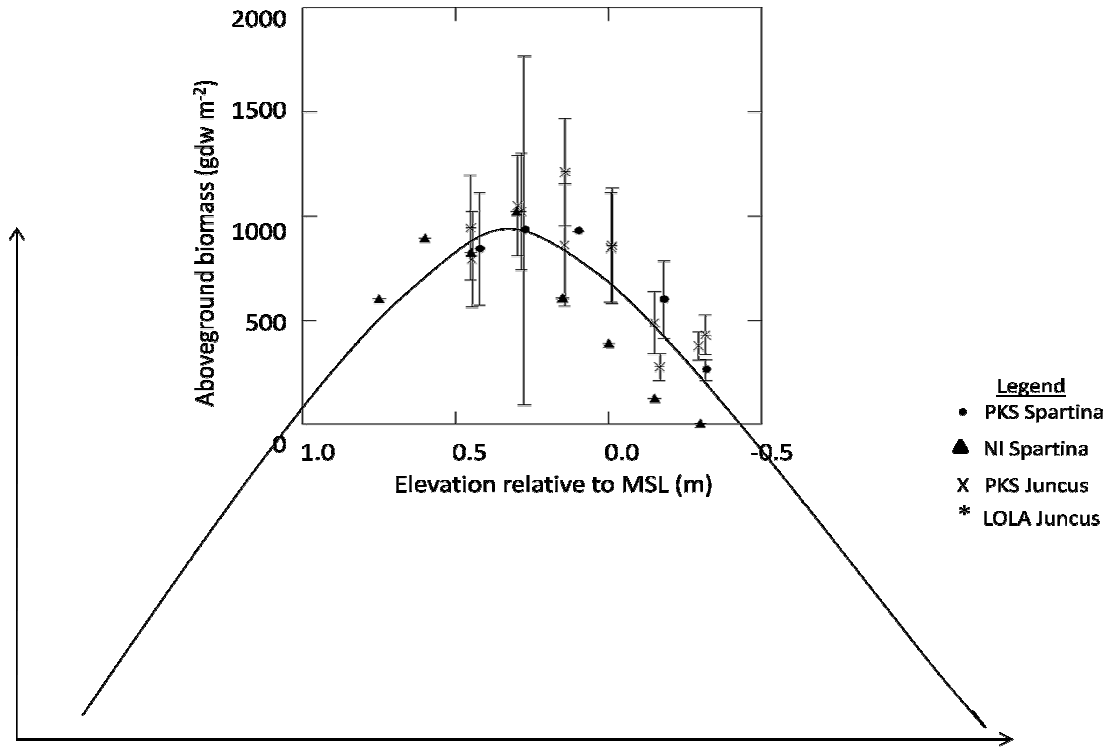


Figure 2.12. EOS aboveground biomass of *Spartina* and *Juncus* cultivated in marsh mesocosms in NC (this study) and in North Inlet (NI), South Carolina

Morris et al. (2002) proposed a model suggesting that inundation regulates macrophyte production and subsequently the ability of marshes to accumulate sediment to maintain elevation relative to sea level. Marshes positioned at an elevation that is sub-optimally inundated produce greater biomass with greater inundation and consequently have the ability to trap more sediments to equilibrate marsh elevation relative to sea level (Morris et al. 2002). Alternately, marshes positioned at an elevation that is supra-optimally inundated produce less biomass with greater inundation and are therefore unable to maintain elevation relative to sea level (Morris et al. 2002). Marshes that are sub-optimally and supra-optimally inundated (suboptimal elevation) are represented on the left and right side of the production- inundation curve, respectively (Figure 2.11). Within the framework of this model, our results indicate that NC marshes dominated by *Spartina* and *Juncus* fall on the right-hand side of the curve and are likely unstable (as per Morris et al. 2002, Figure 2). Their model predicts that macrophyte aboveground biomass will decline with greater inundation as RSLR increases. Exacerbating the predicted scenario is the fact that the sediment budgets of NC estuaries are generally relatively low (Wells and Kim 1989, Phillips 1992). Surface erosion at PKS was evident by the fact that feldspar marker horizons (for Surface Elevation Tables) could not be maintained in experimental plots intended to measure surface accretion. Fragoso and Spencer (2008) have also reported a positive correlation between shallow surface sedimentation and macrophyte production, yet cite a different mechanism. Fragoso and Spencer (2008) found that *S. anglica* production and vegetative renewal was positively correlated to burial of the basal meristem by sediments. Despite the mechanism, the

eroding status of NC marshes is in part due to many NC estuaries having relatively low inorganic sediment budgets. In such a scenario, even marshes with abundant stem/leaf densities would have little sediment available to trap, thus, limiting accretion via sedimentation. This highlights the importance of biogenic accretion processes in some marsh ecosystems, like those of the Albemarle-Pamlico Sound, NC.

The depth of the tidal prism, particle density and settling rate are among the major components that determine the quantity of sediment available to become entrapped and retained upon the marsh surface and are important factors in the ability of marsh habitat in maintaining elevation relative to rising sea level (as per Morris et al. 2002). Accretion mechanisms, explicitly sedimentation, may operate in different ways within astronomically- and meteorologically- dominated inundation regimes. Krone's (1985) concept of the inundation depth being proportional to the quantity of sedimentation may be true only for astronomically-dominated inundation regimes, where each tidal prism that covers the marsh surface has been recharged of sediment from the estuarine source. Under irregularly- or meteorologically- dominated inundation regimes, a given flooding event may deposit sediment from only one tidal prism, yet the marsh surface may remain flooded for an extended period of time. Because marsh ecosystems that occur within meteorologically-dominated inundation regimes are likely to receive less sedimentation on a regular basis, biogenic accretion is necessarily a more important factor here in determining the surface elevation. Conversely, the proportion of inorganic sedimentation occurring on marshes may take place during the irregular pulses of coastal storms (Leonard et al. 1995; Reed 2002).

Belowground biomass

Marsh macrophytes contribute to the vertical accretion of the marsh platform through direct additions of macro organic matter via root growth (Turner et al. 2000, Blum 1993, Blum and Christian 2004, Nyman et al. 2006). The role of sub-surface organic accumulation may be more significant for *Juncus*-dominated marshes than for *Spartina*-dominated marshes as observed from the root dynamics of each species (Appolone 2000, Blum and Christian 2004) and as suggested by the relatively lower bulk densities and higher organic matter content of *Juncus* marsh substrate (de la Cruz and Hackney 1977, Stout 1978). Belowground biomass generally reflected the growth response patterns observed in aboveground material in this investigation. However, belowground production was inversely related to inundation period in a linear pattern, as compared to the curvilinear pattern of the aboveground production. We observed roots extending greater than one meter in length in planter pots receiving minimal inundation. Below the initial macrophyte plugs (including 30 cm of marsh sediments), pots were filled with sand that may not have been saturated, thus providing elevated pipe soils more aerobic edaphic conditions relative to the platform. Our results show that belowground biomass is positively correlated with elevation and are consistent with the basic botanical phenomenon of root growth expanding toward water (Schulze et al. 1996) and nutrients (Darby and Turner 2008) when such resources are limiting to plant growth. In addition, our results concur with other observations of belowground biomass increasing with elevation on marsh platforms (Blum 1993, Widdows et al. 2008). Collectively, these observations suggest that the greatest macro-organic matter contributions are made at

higher elevations and that these contributions could account for a greater proportion of vertical accretion in high marsh zones. This bioaccretion process may be especially critical for marshes to keep pace with sea level rise in estuaries where little inorganic sediment is available. Belowground biomass has been implicated as an indicator of marsh resiliency and recovery and its predictive ability may be superior to that of aboveground biomass (Boyer et al. 2000, Turner et al. 2004, Edwards and Mills 2005, Simenstad et al. 2005, Peterson et al. 2008b). Hence, if belowground biomass is key in predicting the fate of marsh habitat under a scenario of rising sea level, our data suggest that as marshes become inundated for longer periods, they will become less stable if deprived of an inorganic sediment supply.

Juncus response to compare inundation regime

Comparing the response of *Juncus* by inundation regime showed only modest differences between astronomically-dominated and meteorologically-dominated flooding with generally less production at the astronomically-dominated site. The differences that did occur in *Juncus* between the two inundation regimes (EOS live and seasonal change in aboveground biomass, seasonal change in density and leaf green: brown) were observed at elevations at which *Juncus* typically occurs on the adjacent marsh platforms. Marsh platforms occur generally at an elevation approximating MHW (Myrick and Leopold 1963, Redfield 1972, Krone 1985, Zedler et al. 1999). This assumption and our water-level data suggest that rows 2, 3 and 4 of the PKS *Juncus* planter, that were vertically positioned at elevations (-0.08 to 0.1 m relative to MSL; MHW = 0.03 m relative to MSL at PKS), probably received the greatest wind-induced wave activity,

hence, potentially reducing the amount of net production observed. These are the same elevations at which *Juncus* naturally occurs on the marsh platform, but are located away from the estuarine edge at PKS. At both research sites, the planters were positioned just beyond (seaward of) the natural marsh platform and thus all planter-cultivated macrophytes were grown in a higher energy environment relative to those on the adjacent marsh platform. In addition, the PKS site was more energetic on the whole as compared to LOLA, due to astronomical tides, greater wind-induced wave activity and greater localized fetch. Despite the difference in energy regimes at our two research sites, the growth response of *Juncus* differed significantly only at the elevations positioned to receive maximum wave energy.

Zonation of *J. gerardi and J. roemerianus* within the marsh platform has been found to be driven by inundation and salinity (Bertness 1991, Bertness and Pennings 2000, Pennings et al. 2005), despite observations of *Juncus* growing along the estuarine edge of marsh platforms in quiescent areas of estuaries such as in Albemarle, Currituck and Pamlico Sounds, NC (Wilson 1962, Stout 1984, Brinson 1991, this study). Our results show that *Juncus* production decreases with increasing inundation in both semi-diurnal and irregularly-flooded inundation regimes and that *Juncus* production may be negatively impacted by the long-term disturbance or the repeated press (Bender et al. 1984, Glasby and Underwood 1995) of wind-driven wave activity (and perhaps other high energy regimes). The lack of *Juncus'* resilience to this repeated press disturbance could explain observations of *Juncus*-dominated marshes being fringed by *S. alterniflora* in astronomically-dominated estuaries and contrasting observations of *Juncus* growing up

to the estuarine edge in meteorologically-dominated marshes, where overall energy regimes are relatively lower. In mesocosms, *J. roemerianus* yielded greater seasonal production within a meteorologically- versus astronomically- dominated inundation regime at elevations at which it naturally occurs within the coastal landscape.

Validity of multi-level planters

The aboveground growth response of vegetation in the marsh planters reflected that of each given species, site and elevation within the adjacent marsh platform (Figure 2.10). End-of-season aboveground biomass values generally did not differ significantly between macrophytes grown in the planter and platform among like elevations, where those comparisons were possible (Table 2.4) and when compared to other like biomass samples harvested for other studies at each site. The only treatment that differed significantly between the planter and platform was observed in the most inundated row of *Spartina* at PKS. We noted that the platform plot that we thought experienced 81% inundation was established in a sparesely vegetated depression upon the marsh surface approximately 5 m from the estuarine edge and was the lowest point on the platform adjacent to the marsh planters. We chose to establish a platform plot at this location because its unique elevation was the same as row 1 of the *Spartina* planter, however, we recognize that this plot was likely inundated less frequently than row 1 of the planter due to its depressed position in the marsh and plants colonizing this plot likely experienced little inter- or intra- specific competition. In mesocosms, there was generally lower *Juncus* EOS biomass at the astronomically-dominated site (PKS) when compared to that of the meteorologically-dominated site (LOLA). The PKS site was located in an area that

was exposed to fetch from northerly winds and some boat traffic and thus experienced a greater degree of wave energy (in addition to semi-diurnal tidal energy) as compared to the LOLA site. Hence, the extra energy experienced by vegetation in the planters at the PKS, the astronomically-dominated site, could reasonably explain observations of lower net production.

In the marsh planters, macrophytes were grown over a range of elevations equivalent to and extending beyond those of the adjacent marsh platform (and thus receiving inundation periods analogous to the natural platform, where possible). We expected edaphic conditions of the planters to correspond to those of like elevations on the adjacent platform. Other important hydrological aspects are assumed to have occurred comparably at the planter and the adjacent platform (i.e., precipitation, percolation, evapotranspiration, etc.). The plastic pipes of the marsh planters obstructed lateral flow; thus, the macrophytes in planter pots most likely experienced less lateral flow and greater vertical flow relative to a given elevation on the platform. In effect, the tops and bottoms of the plastic pipes were the only sites of exchange for each planter pot. Planter pipes likely received lesser (lower elevations) or greater (higher elevations) degrees of drainage relative to the marsh platform. Thus, although we did not measure the hydraulic-head, this variable presumably differed between the planter and platform at any given elevation. Assuming that vertical water movement is more influential than lateral movement in the planters (as compared to the more hydraulically-isolated marsh platform), tidal pumping may be a more important driver of exchange in the planters. Hence, edaphic conditions in the planter pots were likely more anaerobic at lower

elevations and more aerobic at higher elevations, relative to those at analogous elevations on the adjacent marsh platform. We had not anticipated that we would alter edaphic conditions in a manner different from that which the platform experienced, as this was not apparent in previous planter studies (Morris pers. comm.). Differences in tidal range (tidal pumping) and its effect on edaphic conditions may, in part, explain differing trends in the aboveground production of *S. alterniflora* cultivated in planters at the NC research sites (PKS and LOLA) and those at North Inlet, SC (Morris et al. 2002) and Plum Island, MA (Morris and Sundberg 2008, pers. comm.). The NC sites experienced a relatively smaller tidal range and thus, less pumping to aerate substrate. In addition, we realize that relative position of the mesocosm within the tidal frame is critical in determining inundation period as noted by Morris and Sundberg (2008). Therefore, the relative position of NC planters within the tidal frame may have been lower than for other studies. Nevertheless, neither *Spartina* nor *Juncus* occurred naturally at the extreme elevations achieved by the planters, yet our results may allow us to predict macrophyte response to inundation period and inundation thresholds.

We were surprised to find that our multi-level planter results exhibited trends that differed from those of previous studies using the same planter design. These conflicting results motivated us to expand our mechanistic thinking and propose a conceptual model to aid in resolving the relationship between macrophyte production and inundation. The differing trends in production response to inundation were likely due to a planter's relative position within the tidal frame. Our results were similar to those of North Inlet, SC when relating *Spartina* aboveground production to elevation relative to MSL (Figure

2.12). To date, only site-to-site comparisons of *S. alterniflora* are possible. We believe that we are the first investigators to cultivate *J. roemerianus* in the multi-level planters. The multi-level planters allowed us to manipulate effectively the inundation period for each treatment.

CONCLUSION

Estuarine inundation appears to function as both a subsidy and stressor to marsh macrophytes. The nature of this relationship is determined by the degree of inundation and inundation regime. In general, aboveground biomass elicited a curvilinear relationship to inundation, while this relationship with belowground biomass was linear. Two important macrophytes in the US South Atlantic and Gulf Coast marshes, *Spartina* and *Juncus*, exhibited peak aboveground biomass when inundated between 0.5 to 14% and 0.4 to 28%, respectively, when cultivated in marsh mesocosms. In this investigation, the inundation period threshold for *Spartina* and *Juncus* production occurred at 67% and 42%, respectively, within an astronomically-dominated inundation regime, and at 53% for *Juncus* within a meteorologically-dominated regime. The growth response of *Spartina* and *Juncus* to inundation period was similar; however, *Juncus* exhibited signs of greater stress within the astronomically-dominated inundation regime.

Our results show that marsh macrophytes cultivated in the multi-level marsh mesocosms reflect the growth patterns of macrophytes on the local platform, although we suspect that edaphic conditions in mesocosm differed somewhat from the platform. The marsh mesocosms allowed us to alter effectively the elevation, and therefore inundation period, of macrophytes and we believe that this research has advanced the understanding of the macrophyte inundation-production relationship. We have proposed a conceptual model to describe the relationship of marsh macrophyte production to inundation period. There appears to be an optimal degree of inundation for macrophyte production; this optimum is likely species specific. If macrophytes are sub-optimally inundated,

increased inundation will serve as an energy subsidy resulting in an increase in production. If macrophytes are supra-optimally inundated, increased inundation will serve as a stressor resulting in a decrease in production (Figures 2.11 and 2.12). More research is needed to elucidate the character of macrophyte growth response (i.e., changes in height or density) within the context of the stress-subsidy-stress gradient.

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Chapter 3. SPARTINA ALTERNIFLORA AND JUNCUS ROEMERIANUS: INUNDATION, DISTURBANCE AND SYMBIOSIS

Abstract

Within two hydrodynamically-different inundation regimes in North Carolina, the growth response of and interaction between *Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele to inundation period were evaluated. The species were cultivated jointly in mesocosms over a range of inundation periods, and groundcover changes were assessed after a pulsed disturbance where these species are naturally delineated on the marsh platform. In multi-level mesocosms, end-of-season live aboveground biomass of both species was inversely related to inundation period with no species interaction. Live aboveground biomass was significantly greater in a relatively lower energy inundation regime for both *S. alterniflora* ($P = 0.02$) and *J. roemerianus* ($P < 0.001$) over one growing season, with *J. roemerianus* exhibiting an interaction between inundation period and regime. *Spartina alterniflora* consistently showed greater growth than *J. roemerianus* in most treatments. In platform plots, a significant decline in *J. roemerianus* and encroachment of *S.alterniflora* was observed after a cutting disturbance in both regimes over 16 months. These findings suggest that *S.alterniflora* is significantly more resilient to physical disturbance than *J. roemerianus*, although each responds similarly to inundation period.

Introduction

The zonation of vegetation is a common feature of salt marshes and involves a complex of abiotic and biotic factors. Marsh ecosystems are uniquely positioned within the coastal landscape occurring along the terrestrial-aquatic estuarine interface. Coastal salt and brackish marshes are inherently low in macrophyte diversity because relatively few species can tolerate the physical stressors of varying salinity and frequent inundation experienced by this habitat. The degree to which abiotic factors, such as the degree of inundation and soil salinity (Pennings and Callaway 1992), form a gradient with distance from the estuarine shoreline differs by site and factor, and these factors vary with latitude (Bertness and Pennings 2000, Pennings et al. 2003, Pennings et al. 2005). Zonation is better defined in marshes with steep gradients of salinity (Adams 1963) or inundation (Chapman 1974, Bertness and Ellison 1987, Bertness and Pennings 2000) than in marshes with weak or irregular tidal signals where macrophyte dominance is patchy (Kruczynski et al. 1978, Costa et al. 2003). Examples of heterogeneous zonation are found in some mid-Atlantic marshes, where *Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele each dominate in a mosaic of random monotypic patches at densities that favor *S. alterniflora* and *J. roemerianus* in the low and mid marsh zones, respectively (Brinson and Christian 1999, chapter 2 this thesis). It is assumed that the presence or dominance of species with overlapping environmental tolerance is further defined by interspecific competition (Bertness 1991).

Spartina alterniflora and *J. roemerianus* are among the dominant macrophytes of tidal and brackish, irregularly flooded marshes, respectively, along the Mid and South

Atlantic and Gulf Coasts (Eleuterius 1976, Mitsch and Gosselink 2000); these regions comprise approximately 90 % of the U.S. total marsh acreage (NOAA 1990, Watzin and Gosselink 1992). Despite the dominance and abundance of these macrophytes, their zonation patterns are not fully understood. Generally, *S. alterniflora* occurs along the lowest terrestrial elevation, characteristically dominating the intertidal zone, and exhibits declining aboveground production and ability to dominate at higher elevations where flooding is less regular (Bertness and Pennings 2000, Mitsch and Gosselink 2000). Nevertheless, the elevational distribution of *S. alterniflora* expands locally in range with increasing mean tidal range (McKee and Patrick 1988). *Juncus roemerianus* tends to dominate at slightly higher elevations under irregularly flooded conditions, but it can also be found in areas of more regular flooding (Woerner and Hackney 1997, Brinson and Christian 1999). Eleuterius and Eleuterius (1979) determined that inundation period could not explain the abrupt delineation between the monotypic zones of *S. alterniflora* and *J. roemerianus* found in a Mississippi salt marsh. In Georgia marshes and in greenhouse experiments, Pennings et al. (2005) showed that *J. roemerianus* was limited by physical stresses (flooding and salinity) at its seaward boundary and not by competition, whereas, *S. alterniflora* was limited at its landward boundary by competition with *J. roemerianus*. Brinson and Christian (1999) found the composition of *J. roemerianus*-dominated patches to be stable over a range of elevations in a Virginia marsh with some decrease in biomass in the most-frequently inundated zone; this lower zone also experienced relatively greater disturbance from wrack deposition. Wrack deposition disturbance was the more dominant factor in the decline of *J. roemerianus* in a

study designed to distinguish between the impacts of inundation and this disturbance (Tolley and Christian 1999) at this marsh. Considering that a complex of abiotic and biotic factors dictate marsh zonation, how will the relationship between *S. alterniflora* and *J. roemerianus* change with the increased inundation inherent to sea-level rise?

Even though marsh ecosystems have evolved to be resilient to abiotic stressors, press (e.g., sea-level rise) and pulse (e.g., wrack deposition) disturbances (Bender et al. 1984), which operate on smaller scales, can alter community structure and consequently initiate a change in ecosystem state (Brinson et al. 1995, Christian et al. 2000, Turner et al. 2003). The press of a gradual increase in inundation is strongly associated with the landward encroachment of low-marsh species into high-marsh zones (Orson et al. 1987, Brinson et al. 1995, Donnelly and Bertness 2001, Reed 2002). Similarly, pulsed events such as storm-induced wrack deposition (Bertness and Ellison 1987, Knowles 1991, Brewer et al. 1998, Pennings and Richards 1998, Tolley and Christian 1999), sediment deposition (Ford et al. 1999, Leonard et al. 2002, Voss 2006), fire (Schmalzer et al. 1991) and faunal corridors (Keusenkothen and Christian 2004) can also change marsh community structure, although this change may only be temporary. Within the convergence of the low and high marsh zones of southern US marshes, the cause of the sharp delineation between *S. alterniflora* and *J. roemerianus* monotypic zones is unclear (Eleuterius and Eleuterius 1979, Brinson and Christian 1999, Pennings et al. 2005). This abrupt change in vegetation cover does not appear to occur due to inundation period (Eleuterius and Eleuterius 1979) as inundation and salinity gradients are diffuse across the marsh surface. Increasing water levels will gradually transform the hydrogeomorphic

settings within marshes, promoting a shift in ecosystem state; however, transitions in state may be accelerated by pulse disturbances (Brinson et al. 1995, Christian et al. 2000, Turner et al. 2003). The storm-driven deposition of wrack reduces the percent cover of *Juncus* spp. (*J. roemerianus* and *J. gerardi* in the southern and northern US, respectively) that dominate the high-marsh zone yielding to the expansion of competitively subordinate species (e.g., *S. alterniflora*, *S. patens, D. spicata*) that better tolerate stressful environmental conditions (Reidenbaugh and Banta 1980, Knowles et al. 1991, Valiela and Rietsma 1995, Brewer et al. 1998, Pennings and Richards 1998, Tolley and Christian 1999, Minchinton 2002, Pennings et al. 2005). Under a scenario of rising sea level, erosional processes, salt intrusion, wrack deposition, storm disturbances and root collapse can cause an ecosystem state change whereby a *J. roemerianus*-dominated marsh becomes dominated by *S. alterniflora* (Christian et al. 1990, Brinson et al. 1995, Brinson and Christian 1999, Christian et al. 2000).

Biotic interactions concurrently influence the zonation of marsh macrophytes as the abiotic conditions change with sea-level rise. Some researchers propose that there is an inverse relationship between the competitive ability and stressor tolerance of species (Grime 1974). According to this paradigm, competitively superior species occupy the least stressful zones and displace competitively inferior species to more stressful zones (Bertness 1991, Bertness 1992, Pennings and Bertness 2001, Pennings et al. 2005). This pattern is less apparent where abiotic variables fail to form consistent gradients across the marsh platform, such as observed in irregularly flooded marshes (Costa et al. 2003). Facultative interactions influencing macrophyte zonation have also been demonstrated.

In a New England high marsh, Bertness (1991) found that *Juncus gerardi*, the competitive dominant macrophyte, was facilitated by the presence of *S. patens* and *D. spicata* where these macrophytes mitigated the effects of higher salinity. In a Georgia marsh, Pennings et al. (2005) found *J. roemerianus* to be competitively dominant, yet to facilitate *S. alterniflora* under flooded conditions. Bertness (1991) proposes that secondary succession may be driven by facilitations in harsh physical environments, but that competitive symbioses dominate under benign conditions (Bertness and Shumway 1993).

In this study, I focus on the species-level response at the *S. alterniflora* - *J. roemerianus* marsh interface to extrapolate how processes at the community level might offer insight on marsh zonation and the transformation of a high marsh state to a low marsh state. From the Maryland coast southward to the Texas coast, the dominance of *S. alterniflora* and *J. roemerianus* serve as practical indicators of the hydrogeomorphic setting of many high and low salt/brackish marshes, respectively (Eleuterius 1975, Brinson et al. 1995, Mitsch and Gosselink 2000). Marshes dominated by *S. alterniflora* and *J. roemerianus* each possess some distinguishing features. *Spartina alterniflora* tends to dominate the intertidal, low-marsh zone where regular estuarine inundation contributes mineral-based sediments, acts to maintain soil salinities and exchanges nutrients, toxins and organic matter within this area of the marsh (Brinson et al. 1995, Bricker-Urso et al. 1989, Christian et al. 1990, Mendelssohn and Morris 2000, Morris et al. 2002, Christian et al. 2000, Christiansen et al. 2000, Nyman et al. 2006). *Juncus roemerianus* tends to dominate the irregularly flooded, high-marsh zone where

meteorological and terrestrial hydrological sources have greater influence, bioaccumulation dominates accretion and estuarine exchanges occur less frequently (Brinson et. al 1995, Bricker-Urso et al. 1989, Cahoon et al. 1998, Brinson and Christian 1999, Nyman et al. 2006). Studies of nutrient budgets suggest that tidal input is the chief nitrogen source for the low-marsh zone (Gallagher et al. 1980, Thomas and Christian 2001); however, nitrogen fixation and denitrification also occur here (Sherr and Payne 1978, de Souza and Yoch 1997, Teal et al. 1979, Kaplan et al. 1979). With fewer inputs, nitrogen cycling in the high marsh is greater than compared to that in the low marsh (Thomas and Christian 2001). Habitat utilization of low and high marsh zones differ where the more frequently inundated intertidal zone is important for aquatic species for foraging and refuge (Kneib 1987, Hettler 1989, Fitz and Wiegert 1991, Halpin 2000, Craig and Crowder 2000). However, the irregularly inundated high marsh may serve as key nursery habitat to species that benefit from prolonged spring and fall inundation (Stout 1984, Marraro et al. 1991, Voss 2006). Peterson and Turner (1994) found that marsh edge zones were used by both resident and transient aquatic faunal species while interior marsh zones were chiefly used by resident species. The habitat complexity provided by the diversity of marcrophytes found in state-change transition zones may benefit marsh nekton that are able to profit from the expanded variety of habitat functionality in close proximity (Crowder and Cooper 1982, Rozas and Reed 1993).

Inundation period, salinity level and disturbance are among the chief mechanisms believed responsible for the zonation of *S. alterniflora* and *J. roemerianus* on the marshes where these species dominate. In this study, I attempt to address the effect of inundation

period on macrophyte growth patterns when co-planted, using multi-level marsh planters (explained in chapter 2). I established multi-level marsh planters at two hydrodynamically different locations to observe effects of inundation regime; I also expect salinity differences between the two sites chosen. Lastly, I assessed the interactive response of these dominant macrophytes to a pulsed disturbance event on the marsh platforms. Here, experimental plots were established and monitored along the sharply delineated margin between *S. alterniflora*- and *J. roemerianus*- dominant patches following a cutting disturbance at each site. The objectives of this study were to determine the growth response and interaction of *S. alterniflora* and *J. roemerianus*: (1) to inundation period when cultivated jointly, (2) for comparison of inundation period effect of jointly planted macrophytes by inundation regime and (3) to a pulsed disturbance incurred where they intersect on the marsh platform. To address these objectives, I tested the following hypotheses:

> H^1: *Spartina alterniflora* will show dominant growth patterns over *Juncus roemerianus* in a tidally-dominated inundation regime and at greater inundation periods.
>
> H^2: *Juncus roemerianus* will show dominant growth patterns over *Spartina alterniflora* in a meteorologically-dominated inundation regime and at shorter inundation periods.
>
> H^3: The reduction in aboveground cover will be greater for *Juncus roemerianus* than for *Spartina alterniflora* after the first year following a cutting disturbance.

Methods

Site description

A consequence of the unique geographic features along the North Carolina (NC) coastline results in two basic types of estuarine hydrological regimes, those dominated by semi-diurnal tides and those that are irregularly inundated. The coastal barrier islands of the Outer Banks enclose the Albemarle-Pamlico Estuarine System (APES), the largest lagoonal estuary in the U.S. Here, the few inlets along the Outer Banks limit tidal exchange between the Atlantic Ocean and APES. The watersheds of four major rivers (Chowan, Roanoke, Tar-Pamlico and Neuse) drain much of the NC northern and central coastal plain and flow into the APES. With limited tidal exchange, water levels in the APES are largely dictated by meteorological factors, chiefly wind. In contrast, estuaries along the southern NC coastline are significantly smaller with more numerous inlets that provide great connectivity to the Atlantic Ocean, and are thus dominated by astronomical forces. Of the 105,866 hectares of coastal marshes within NC (NOAA 1990), approximately 60% are dominated by *J. roemerianus* (Wilson 1962). *Spartina alterniflora* generally dominates the shoreline fringe and intertidal tidal zones of NC marsh ecosystems. *Juncus roemerianus* typically dominates the high marsh zones, and it occurs abundantly along quiescent estuarine shorelines.

I established research sites at two points along the central NC coast at Pine Knoll Shores (PKS) (33.6953^{o} N, 76.8417^{o} W) and at Lola (LOLA) (34.9501^{o} N, 76.2796^{o} W) (Figure 3.1).

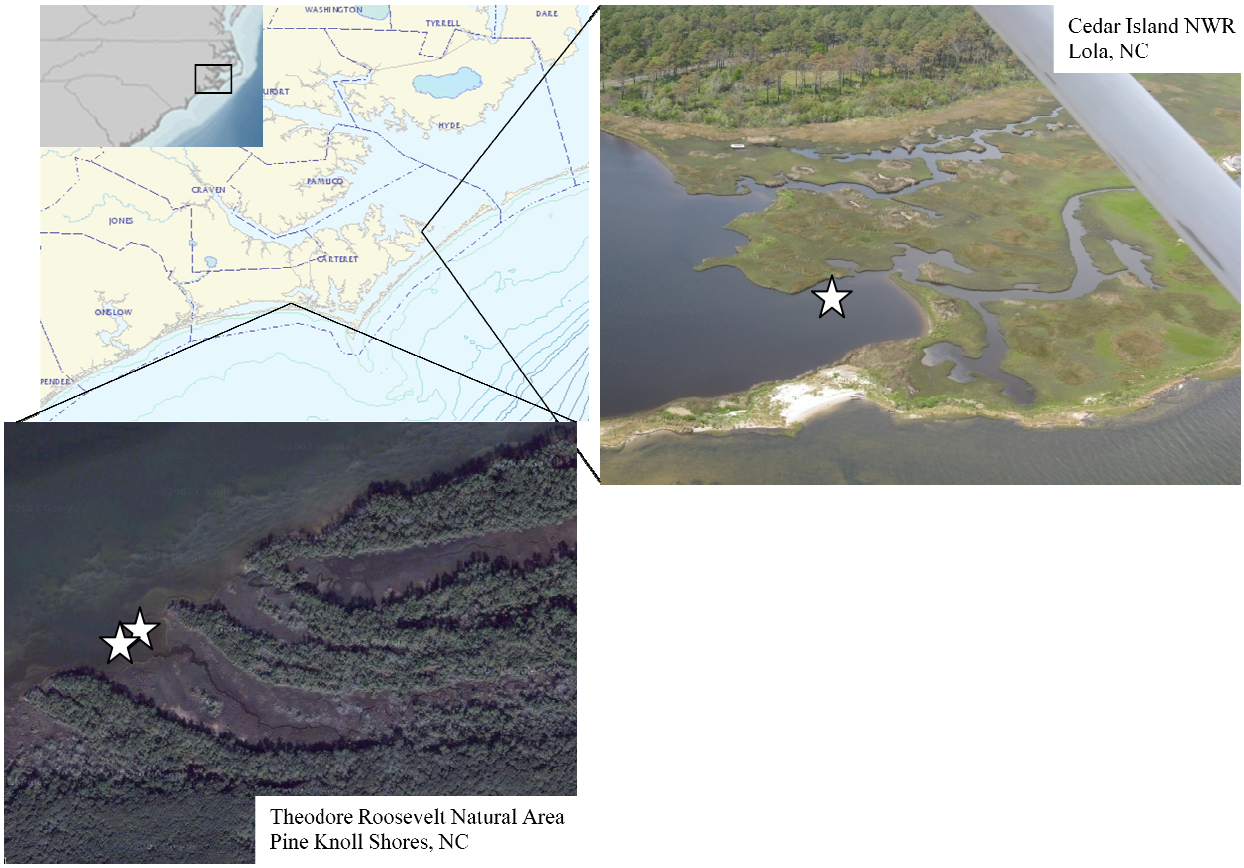

Figure 3.1. Map of NC study area and aerial photo of research sites (stars indicate marsh planter locations)

Sites were spaced approximately 50 km apart and experienced similar meteorological conditions but different tidal regimes. The astronomical tidal range was measured as 60 cm and 8 cm for PKS and LOLA, respectively (chapter 2 this thesis). The dominance of the astronomical tidal signal at PKS is responsible for a regular, semi-diurnal pattern of marsh inundation, although meteorological factors (chiefly wind) are also important. The weak astronomical tidal signal experienced at LOLA results in an irregular pattern of marsh inundation; here, the marsh platform is sometimes dry or flooded for weeks at a time depending on wind speed and direction. Typically, the marsh experienced less wave energy at the LOLA site than at the PKS site; this was likely due to the smaller fetch length of the LOLA site (see discussion). Over the 18-month period of this study, the mean annual salinity was 34 (±1.8) psu and 29 (±4.3) psu at PKS and LOLA, respectively. While low-topographic, erosional geomorphology is common between the research areas, the PKS research site was established on broad, gradually ramping, back-barrier marsh habitat within a dune-and-swale system with few tidal creeks, and the LOLA site was established within an alcove of broad-platform marsh habitat. *S. alterniflora* (hereafter, *Spartina*) and *J. roemerianus* (hereafter, *Juncus*) were each dominant in a mosaic of random patches at each site, with *Spartina* dominating the overall estuarine shore zone at PKS.

Water level record

At each research site, a temporary water level station was established in accordance to the requirements of the National Oceanic and Atmospheric Administration's (NOAA) Center for Operational Oceanographic Products and Services

(CO-OPS) (NOAA 2003, NOAA 2007). The PKS station (34.53436^{o} N 76.83176^{o} W) was established at the dock pier of the NC Aquarium in May 2006, and LOLA station (34.95098^{o} N 76.28112^{o} W) was established at the Lola Road dock (property of US Fish and Wildlife) in June 2006. The North Carolina Geodetic Survey established Second Order Class 2 benchmarks at each site in the proximity of the water level stations. Each water level station consisted of two HOBO (Onset Computer Corp., model: U20-001-01) pressure transducers, one of which measured barometric pressure and the other measured water-column pressure; date, time, temperature and transducer pressure were recorded every 3 minutes and downloaded monthly using the manufacturer's software. At each download and launch, water level relative to station benchmark was recorded for reference; from this, water level relative to NAVD88 and mean sea level (MSL) was later computed. A calibrated Topcon® Model RL-50A rotating-laser system was used for all leveling at the research sites; a Trimble® 5800 RTK GPS system unit was used to verify elevation of a temporary benchmark at the PKS marsh-planter site in February 2008. Post-processing of water-level data was completed using HOBOware® software adjusting to time-referenced, site-specific barometric pressure. Water levels from 23 March through 21 September 2007 were used to determine inundation periods for each site.

Multi-level planters

Multi-level marsh planters, as described in the previous chapter (chapter 2, this thesis), were used to manipulate the elevation and therefore inundation period of co-planted dominant marsh macrophytes (*Spartina* and *Juncus*) (Figure 3.2). Each marsh planter was constructed of 15-cm-diameter PVC pipe, cut and bolted to result in open-

ended “pots” that formed six rows, at 15-cm vertical intervals, ranging from 30 to 105 cm in elevation above the base; there were six replicates per row (Figure 3.2). Planter rows were numbered with row 1 as the most inundated and row 6 as the least inundated. At each site, marsh planters were positioned in the estuarine waters (lowest row facing south) just beyond the marsh platform.

Figure 3.2. Multi-level marsh planter co-planted with *S. alterniflora* and *J. roemerianus* at LOLA adjacent to marsh platform

The lower portion of each planter pot was filled with local estuarine sand and the upper 30 cm contained the *Spartina* and *Juncus* plugs planted in marsh sediments. Source plug material was harvested from the adjacent marsh platform along the *Spartina-Juncus* margin on 13 and 14 April 2007 at PKS and LOLA, respectively. One co-planted planter was established at each site with *Spartina-Juncus* plugs comprised of approximately equal proportions of *Spartina* and *Juncus* with a minimum of 3 *Spartina* stems and 3 *Juncus* leaves in each plug. Another planter was established at PKS as an individually-planted reference for comparison with co-planted pots; here, 3 pots of each elevation containing *Spartina* and the other 3 pots of each elevation containing *Juncus*. Reference and co-planted pots contained approximately equal amounts of vegetation. To discern differences between individually- and co- planted samples, the seasonal or monthly production of individually-planted *Spartina* and *Juncus* from like rows were matched for comparison with co-planted samples. Table 3.1 shows the elevation of all marsh planter rows, relative to NAVD88, mean sea level (MSL) and percent of time flooded during each growing season.

Table 3.1. Elevation (relative to MSL and NAVD88) (m) and inundation periods of marsh mesocosm rows

Marsh planter	row	Elevation relative to MSL (m)	Elevation relative to NAVD88 (m)	Percent time flooded (%)	Inundation (arcsine transformed value)
PKS 2007 *Co-planted*	1	-0.618	-0.500	100.	1.516
	2	-0.472	-0.354	96.	1.369
	3	-0.309	-0.191	75.	1.044
	4	-0.175	-0.057	49.	0.778
	5	-0.023	0.095	24.	0.511
	6	0.130	0.248	7.	0.267
LOLA 2007 *Co-planted*	1	-0.310	-0.310	100.	1.571
	2	-0.157	-0.157	77.	1.065
	3	-0.005	-0.005	36.	0.644
	4	0.143	0.143	12.	0.356
	5	0.294	0.294	2.	0.142
	6	0.355	0.355	1.1	0.105
PKS 2007 *Spartina & Juncus reference*	1	-0.571	-0.453	99.	1.493
	2	-0.427	-0.309	92.	1.292
	3	-0.267	-0.149	67.	0.958
	4	-0.135	-0.017	42.	0.704
	5	0.014	0.132	19.	0.451
	6	0.163	0.281	5.	0.223

Several plant growth variables were measured to quantify macrophyte response to inundation. After a 2-week acclimation period, in each pot, each culm (*Spartina*) or leaf (*Juncus*) was counted and measured for net total length, live length (green portion) and dead length (brown portion) from the stem/leaf base to the leaf tip (tallest leaf tip for *Spartina*). Measurements were repeated on an approximately month basis. At the end of the growing season (EOS), all samples were removed from planter pots on 6 and 7 Sep 2007 at PKS and LOLA, respectively. Here, aboveground biomass from each pot was clipped at the soil surface and placed into labeled bags in the field; in the lab, each culm/leaf length was measured (green, brown and total length), culms/leaves counted and samples were dried at 85^{o}C until weights were stable. The belowground biomass from each pot was placed into labeled bags in the field. At the lab, these samples were first liberated from soil while contained in 1 mm mesh nylon screening using water pressure (hose and nozzle), the length of the three longest roots of each species were identified and measured from base of respective rhizomes, then samples were sieved (via water pressure) using 5.6-mm and 1-mm mesh sieves to separate "live" (5.6-mm mesh) and "dead" (1-mm mesh) material (similar to methods used by Valiela et al. 1976, Gallagher et al. 1988, Darby and Turner 2008). Live and dead belowground fractions were dried and weighed, as were aboveground samples; two sub-samples of each dried fraction were ashed at 500^{o} C for 6 hours to determine organic matter content, thus, belowground biomass data reported here includes only organic matter. To estimate the initial biomass of each species, I multiplied the sum of culm or leaf lengths per pot by the weight-length ratio computed for another component of this study (chapter 2, this thesis). These ratio

values were 0.010904 g cm^{-1} for *Juncus* and 0.024964 g cm^{-1} for *Spartina*. The same ratios were applied to total (green and brown length) biomass and live (green length) biomass computations for each species.

Disturbance plots

On the marsh platform at each site, 2-m X 1-m paired plots were delineated randomly along the *Spartina- Juncus* margin so that a 1-m^2 square quadrat of *Juncus* abutted a 1-m^2 square quadrat of *Spartina* (Figure 3.3). Therefore, each plot consisted of 1 m^2 of *Juncus* and 1 m^2 of *Spartina*. In one of each of the plot pairs, the vegetation was clipped to the ground and removed to simulate a de-vegetation disturbance and the other was undisturbed as a control in the same vicinity. Such a de-vegetation disturbance could occur due to a fire or wrack deposition that denudes the aboveground material from the marsh surface. During sampling, a 1-m^2 enumerated quadrat, divided into one-hundred cm^2 cells, was placed over each plot so that each cell could be repeatedly located and characterized for content of vegetative cover.

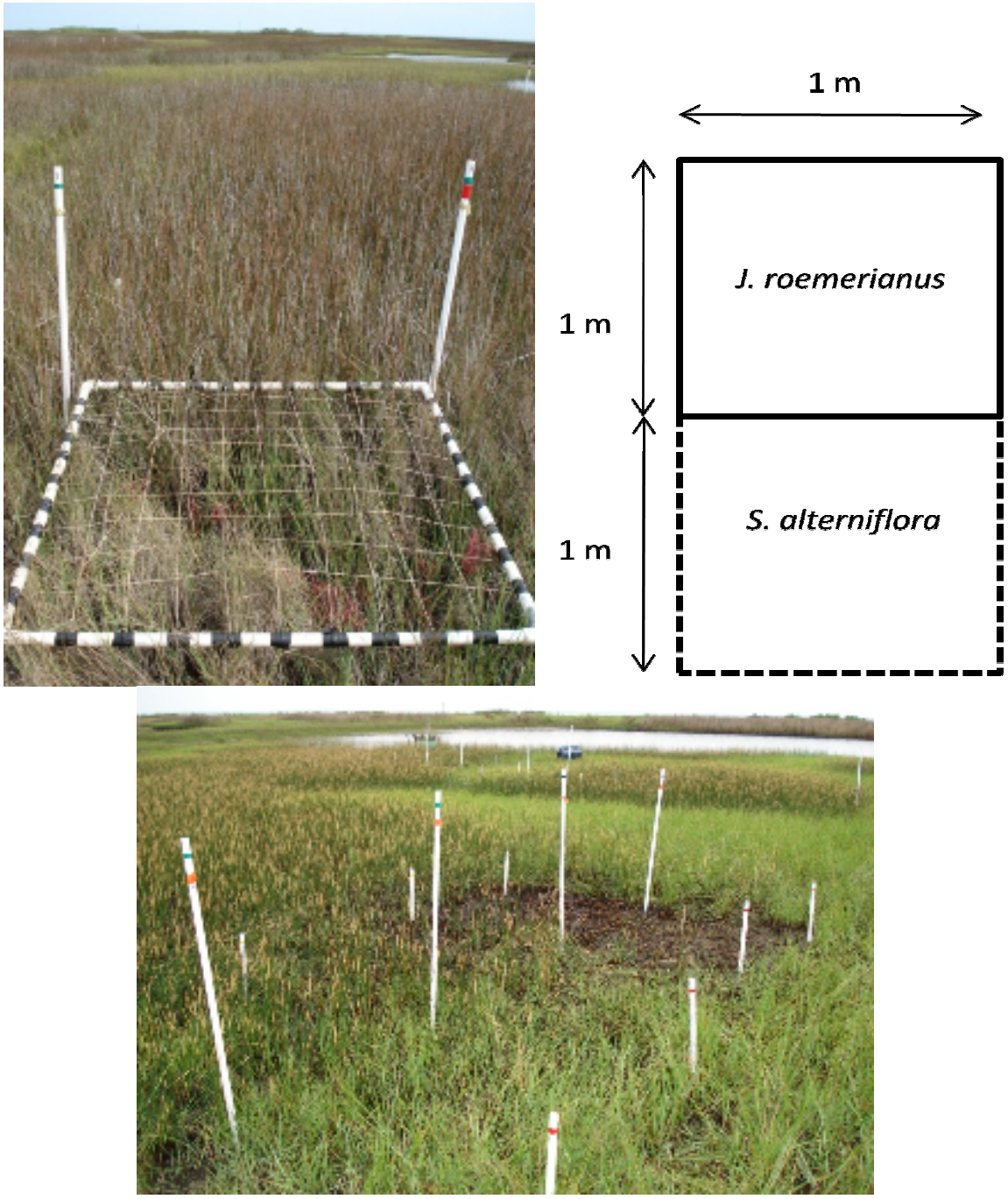

Figure 3.3. Top: Photograph and illustration of a plot delineated along *S. alterniflora- J. roemerianus* margin showing 100 10-cm X 10-cm grid cells within a 1-m^2 *S. alterniflora* quadrat Bottom: Photograph showing control (foreground, left) and cut (right) paired plots in the burnt area at LOLA

The rank-ordered list of species contained within each cell at the surface was logged before the disturbance treatment, and at 2, 12 and 16 months post-treatment. The ground cover of each plot was assessed on 21 May and 11 July 2007, 1 June and 10 October in 2008 at PKS, and on 17 May and 17 July 2007 and 2 June and 12 October 2008 at LOLA. Ground cover classes were recorded as being dominated by *Spartina*, *Juncus*, other species (species noted), or bare substrate. At LOLA, the number of disturbance factors was doubled because areas of the study site had been subjected to fire in February 2007, as part of the USFWS management plan. Hence, I replicated the disturbed cut (primary disturbance) and control paired plots in both burnt (secondary disturbance) and unburnt zones of the marsh. There were a total of 8 plots (4 pairs) established at PKS and 16 plots (8 pairs) established at LOLA for this phase of the study. The presence of wrack was also noted; however, little wrack has been found in our plots to date.

Statistical analyses

SYSTAT ® software (version 11.00.01) was used for statistical analyzes. Inundation period (as proportion of time flooded, Table 3.1), the chief independent variable, was normalized by taking the arcsine of the square root of the proportion of time flooded. The inundation proportion of time flooded was used in figures for the convenience of readers; statistical analyzes utilized the transformed inundation value. Most metrics and indices met the Shaprio-Wilks criteria for normality (Shapiro-Wilks $P \geq 0.10$). A General Linear Model (GLM) was used to assess the statistical significance ($\alpha = 0.05$) of the effect of inundation on macrophyte growth response metrics and indices. Because I found linear relationships in the growth response of *Juncus* and *Spartina* to

inundation when individually-planted in a previous mesocosm study, I expected a similar linear response when co-planted, unless a symbiotic relationship between these species caused an interaction. A repeated measures analysis was used to compare the percent ground cover of *Spartina* and *Juncus* quadrats in control and disturbed (clear cut) plots between treatments (cut and burnt (LOLA only), with in treatments and for interactions between treatments.

Dominance indices

I created three indices to evaluate the relationship between *Juncus* and *Spartina*, each indicates the dominance of one species to another using different response variables. Dominance indices employed only aboveground material because the two macrophyte species were co-planted in pots and belowground material could not be isolated by species appropriately. The first index considers the proportional change in the total aboveground biomass of each relative to one another. Here, the seasonal proportional change in the total aboveground biomass of *Juncus* was subtracted from that of *Spartina* (Equation 1). The second index computes only live aboveground biomass in the same manner (Equation 2). The third index considers the net change in culm (*Spartina*) and leaf (*Juncus*) live (green) length of each species on an approximately monthly basis and then normalizes net length change by the number of days between each sampling period. Here, the monthly net change in *Juncus* live leaf length per pot was subtracted from that of *Spartina* (Equation 3). All indices use the same method for quantifying macrophyte dominance. A value of zero indicates an equal proportional contribution from both species. Values > 0 indicate increasing *Spartina* dominance, and values < 0 indicate

increasing *Juncus* dominance. As a reference for the co-planted pots, data from the individually-planted planter pots were paired within a given inundation treatment so that one *Juncus* pot was matched with one *Spartina* pot. These individually-planted data served as a reference for comparison purposes.

Macrophyte dominance index # 1 =

$$[(B_{SEOS(total)} - B_{Si(total)}) / B_{Si(total)}] - [(B_{JEOS(total)} - B_{Ji(total)}) / B_{Ji(total)}] \quad \text{Equation 1}$$

Where:

$B_{SEOS(total)}$ = end-of-season *Spartina* total (live plus dead) biomass / pot
$B_{Si(total)}$ = initial *Spartina* total biomass / pot
$B_{JEOS(total)}$ = end-of-season *Juncus* total biomass / pot
$B_{Ji\ (total)}$ = initial *Juncus* total biomass / pot

Macrophyte dominance index # 2 =

$$[(B_{SEOS(live)} - B_{Si(live)}) / B_{Si(live)}] - [(B_{JEOS(live)} - B_{Ji(live)}) / B_{Ji(live)}] \quad \text{Equation 2}$$

Where:

$B_{SEOS(live)}$ = end-of-season *Spartina* live biomass / pot
$B_{Si\ (live)}$ = initial *Spartina* live biomass / pot
$B_{JEOS(live)}$ = end-of-season *Juncus* live biomass / pot
$B_{Ji\ (live)}$ = initial *Juncus* live biomass / pot

Macrophyte dominance index # 3 =

$$[LL_{ST2} - LL_{ST1}] - [LL_{JT2} - LL_{JT1}] / T_2 - T_1 \text{ (\# days)} \quad \text{Equation 3}$$

Where:

LL_S = live length of *Spartina* culms / pot
LL_J = live length of *Juncus* leaves / pot
T_1 = start of sampling period
T_2 = end of sampling period

Results

Marsh planters

Spartina and *Juncus* growth patterns each yielded a similar response to inundation when co-planted in marsh mesocosms. The EOS *Spartina* total (live plus dead) aboveground biomass differed significantly with inundation period in all planters ($P \leq 0.011$) (Figure 3.4). The EOS *Juncus* aboveground biomass differed significantly ($P \leq 0.027$) with inundation period only at PKS (co-planted and reference planters), not at LOLA ($P = 0.691$). When considering EOS live only material, *Spartina* aboveground biomass was clearly inversely proportional to inundation period ($P \leq 0.009$) in all planters and that of *Juncus* differed significantly only at LOLA ($P = 0.0006$) also showing a threshold in which EOS live biomass was negligible when inundated ≥ 77% (Figure 3.4).

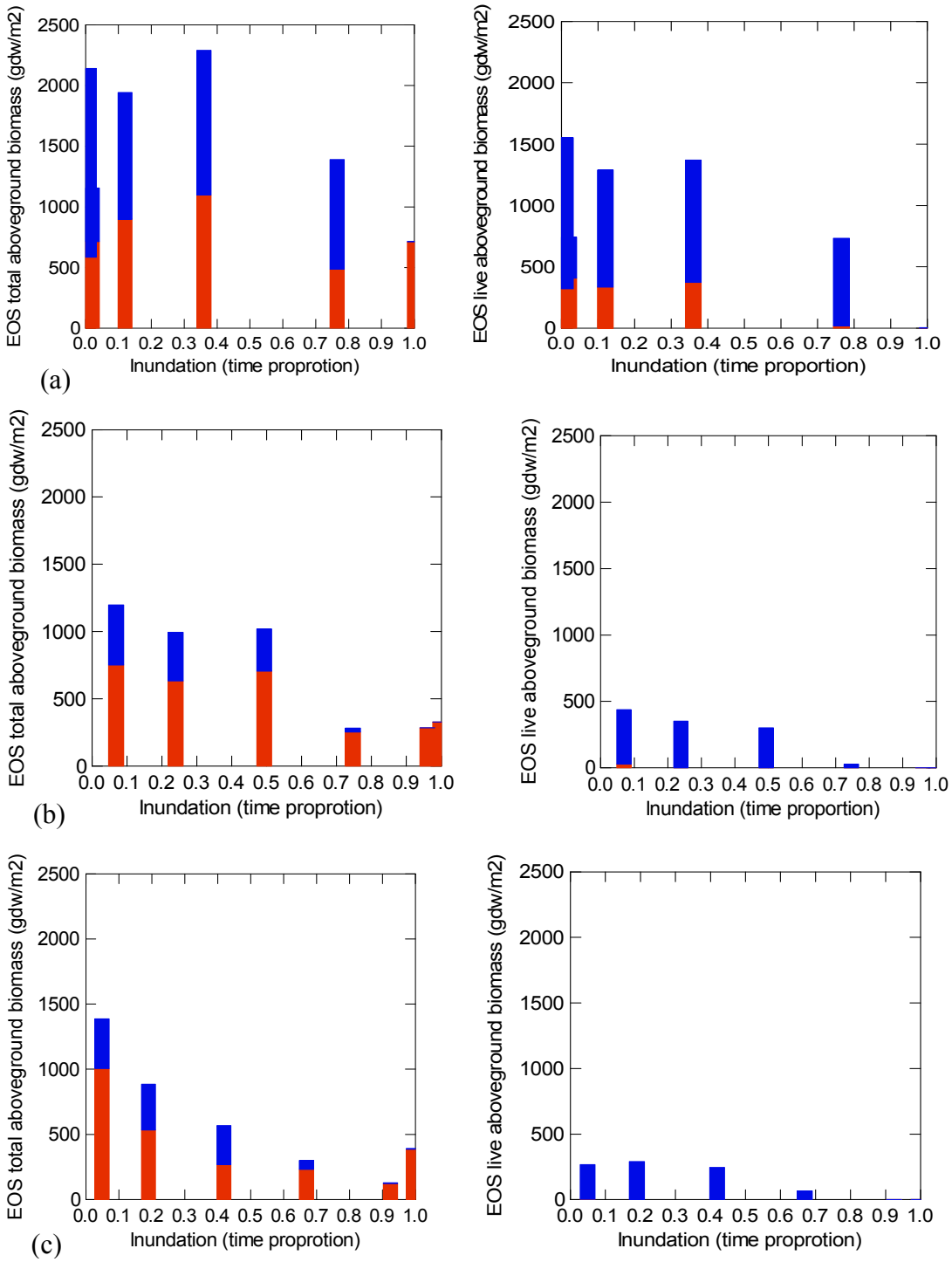

Figure 3.4. End-of-season total (left column) and live (right column) *Juncus* (red) and *Spartina* (blue) in (a) LOLA, (b) PKS and (c) REFERENCE marsh planters

The EOS aboveground net biomass of both *Spartina* and *Juncus* differed by inundation regime. Aboveground production was generally lower in the co-planted and reference mesocosms cultivated at PKS than at LOLA (co-planted mesocosm only). The EOS live aboveground net biomass in co-planted planters differed significantly between sites, differing ($P= 0.017$) and ($P< 0.0001$) for *Spartina* and *Juncus*, respectively, with greater production of both species at LOLA (Figure 3.4). For EOS live *Juncus*, there was an interaction between inundation period and site ($P= 0.003$), due to less live *Juncus* present at PKS. The seasonal change in total aboveground biomass likewise differed ($P= 0.006$) and ($P=0.736$) for *Spartina* and *Juncus*, respectively (Figure 3.5). As noted previously, much of the EOS total *Juncus* biomass consisted of dead material. The three indices were computed to elucidate macrophyte dominance (noted above) did not differ by inundation regime in any case. Therefore, although there was less live *Juncus* at PKS by the end of the season, the overall growth patterns of *Spartina* and *Juncus* were similar between regimes.

The relative growth response of *Spartina* and *Juncus* aboveground material was assessed to examine the influence of inundation period on seasonal growth. The relative seasonal change in total (live and dead) aboveground biomass differed significantly with inundation period for *Spartina* ($P \leq 0.008$) in all three planters, yet not for *Juncus* in any planter (Figure 3.5).

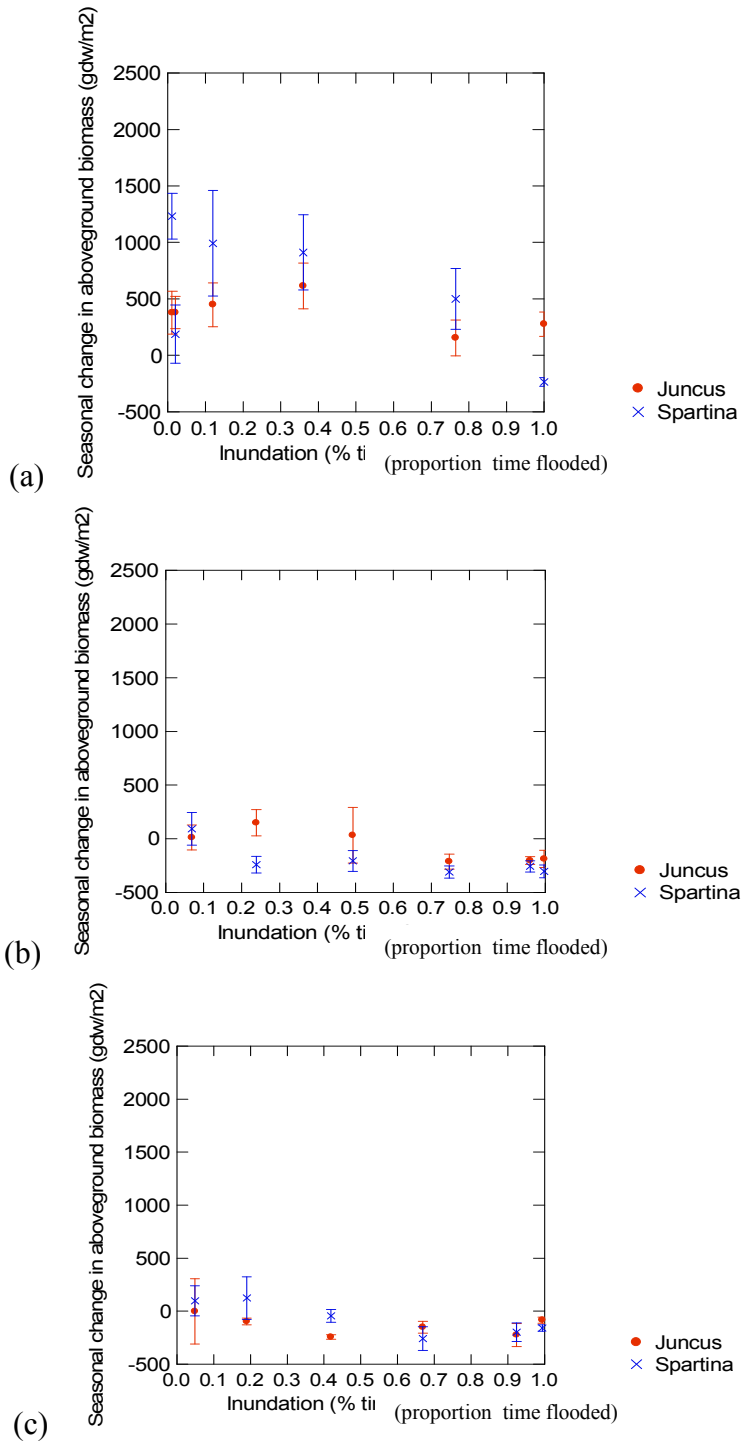

Figure 3.5. The seasonal change in the aboveground biomass of *Juncus* (red) and *Spartina* (blue) in co-planted planters at (a) LOLA and (b) PKS and (c) individually-planted reference planter (mean ± 1 SEM)

There was no interaction between relative seasonal growth of these macrophytes with inundation period. The seasonal proportional change in the total aboveground biomass of *Juncus* was subtracted from that of *Spartina* to yield an index (Equation 1) that was plotted by inundation period (Figure 3.6, left column). Here, a value of zero indicates an equal relative biomass contribution from each species. Values > 0 indicate increasing relative contribution from *Spartina*, and values < 0 indicate increasing relative contribution from *Juncus*. Only the planter with pots of individual species yielded indices that differed significantly (P=0.03) with inundation. Overall, *Spartina* dominance of the relative total biomass was marginal and this dominance decreased with increasing inundation. *Juncus* was dominant in the most frequently inundated treatments. It is important to note that a majority of the biomass of frequently inundated *Juncus* was comprised of dead material. The seasonal increase in *Spartina* stem and *Juncus* leaf density was inversely proportional to inundation period. This response was statistically significant for *Spartina* ($P \leq 0.002$) in all three planters and for *Juncus* in the co-planted planter at LOLA ($P = 0.011$) only (Figure 3.7).

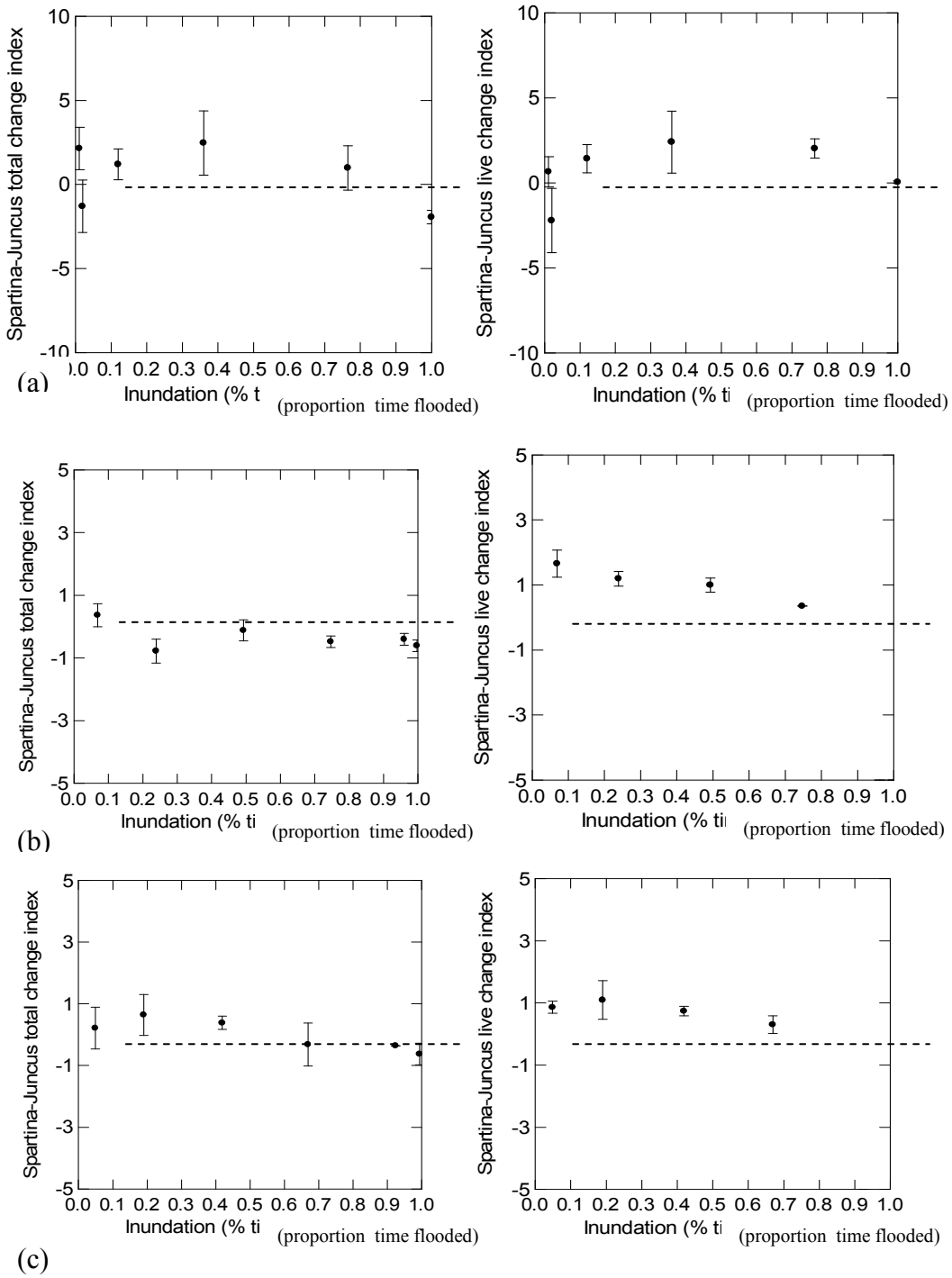

Figure 3.6. Indices of *Spartina – Juncus* seasonal proportional change in total (left column) and live (right column) aboveground biomass in (a) LOLA, (b) PKS and (c) REFERENCE planters (mean ± 1 SEM) Y axis index key: 0 = *Spartina* and *Juncus* contribute equally, values > 0 indicate increasing *Spartina* dominance, and values < 0 indicate increasing *Juncus* dominance [note: Y-axis scales differ in scale]

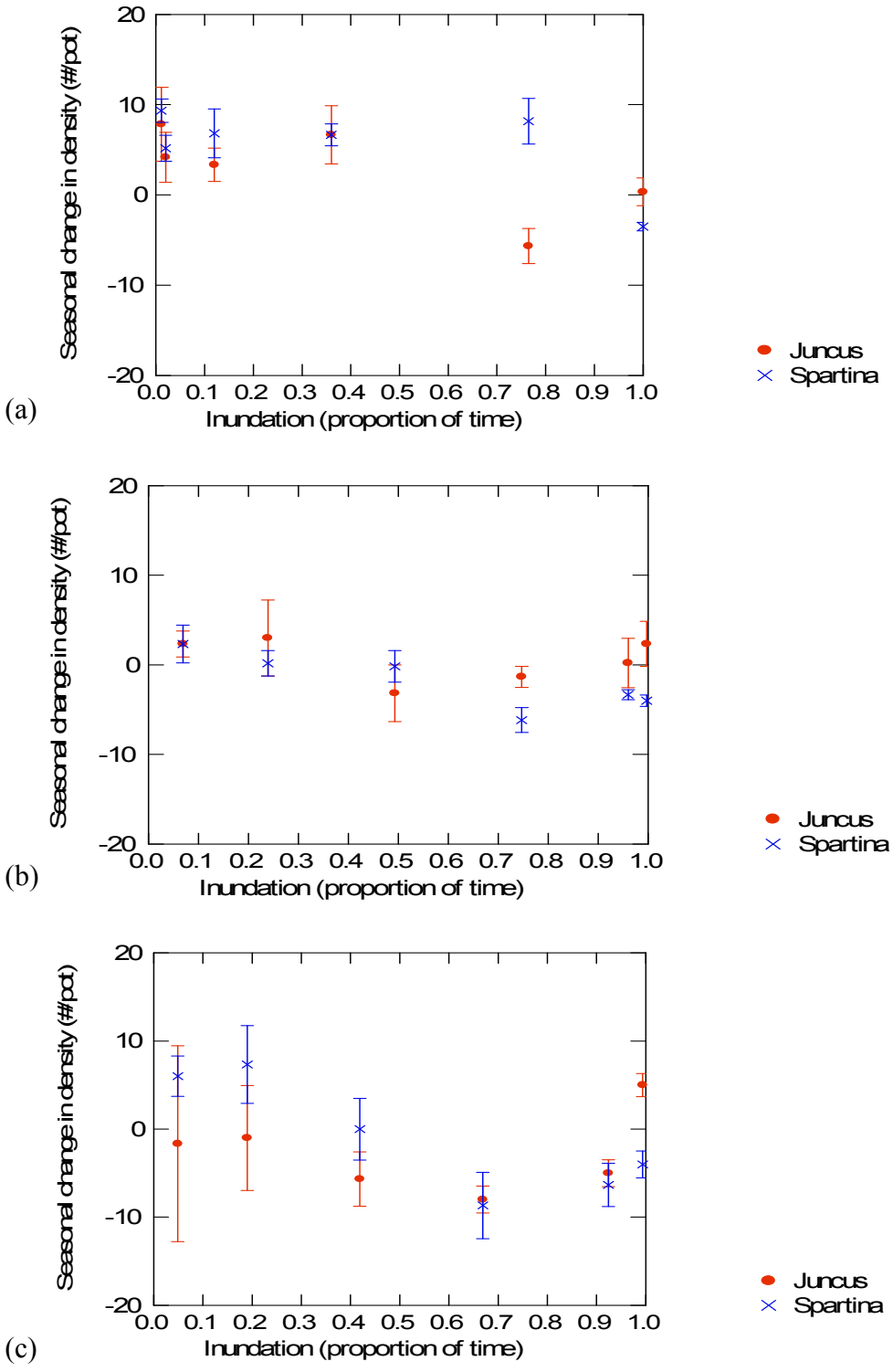

Figure 3.7. The seasonal change in *Juncus* leaf (red) and *Spartina* stem (blue) density in (a) LOLA, (b) PKS and (c) REFERENCE planters

Live aboveground material was analyzed to elucidate differences in the response of *Spartina* and *Juncus* to inundation period and possible species interactions, as this variable describes the current season's growth and may more accurately reflect growth patterns than total biomass. Therefore, the second and third indices were based upon live material only (see methods Equations 2 and 3). The second index evaluated the difference in the seasonal proportional net change in EOS live aboveground biomass between *Spartina* and *Juncus*; these results were similar, but differed statistically from the EOS total aboveground biomass index (as described above) (Figure 3.6, right column). Here, the relative live biomass contribution by *Spartina* was greater than that of *Juncus* in all three planters, with only the PKS co-planted planter index differing ($P=0.027$) by inundation period.

A third index was created to evaluate the relationship between live *Spartina* and *Juncus* aboveground material on an approximately monthly basis. Similar to the previous indices, an increasing relative contribution by *Spartina* yields greater positive values and an increasing relative contribution *Juncus* dominance yields values that are more negative. For the initial April-June period, this index differed significantly ($P \leq 0.026$) with inundation period for both the PKS and LOLA co-planted planters; surprisingly, increasing inundation periods yielded an increasing relative contribution by *Spartina* at LOLA and an increasing relative contribution by *Juncus* at PKS (Figure 3.8). As the season progressed in the co-planted planter at LOLA, *Spartina* increasingly dominated the live aboveground biomass composite, at proportions that were similar among inundation periods. At the end of the season, only two pots in the co-planted planter at

LOLA contained live material at the treatment inundated 100%, with one containing only *Juncus* and the other containing only *Spartina*. Within the PKS co-planted planter, the relative contribution by *Spartina* increased overall throughout the growing season, with greater relative contributions by *Juncus* observed at greater inundation periods in June and July (Figure 3.8). Here, this dominance index differed significantly ($P \leq 0.003$) with inundation period for the entire of the season. The individually planted reference planter (PKS only) initially showed a much greater contribution by *Spartina* live material; this dominance declined as the net growth declined in both *Spartina* and *Juncus*, indicative of increasing stress. A majority of the *Juncus* plants died in this planter.

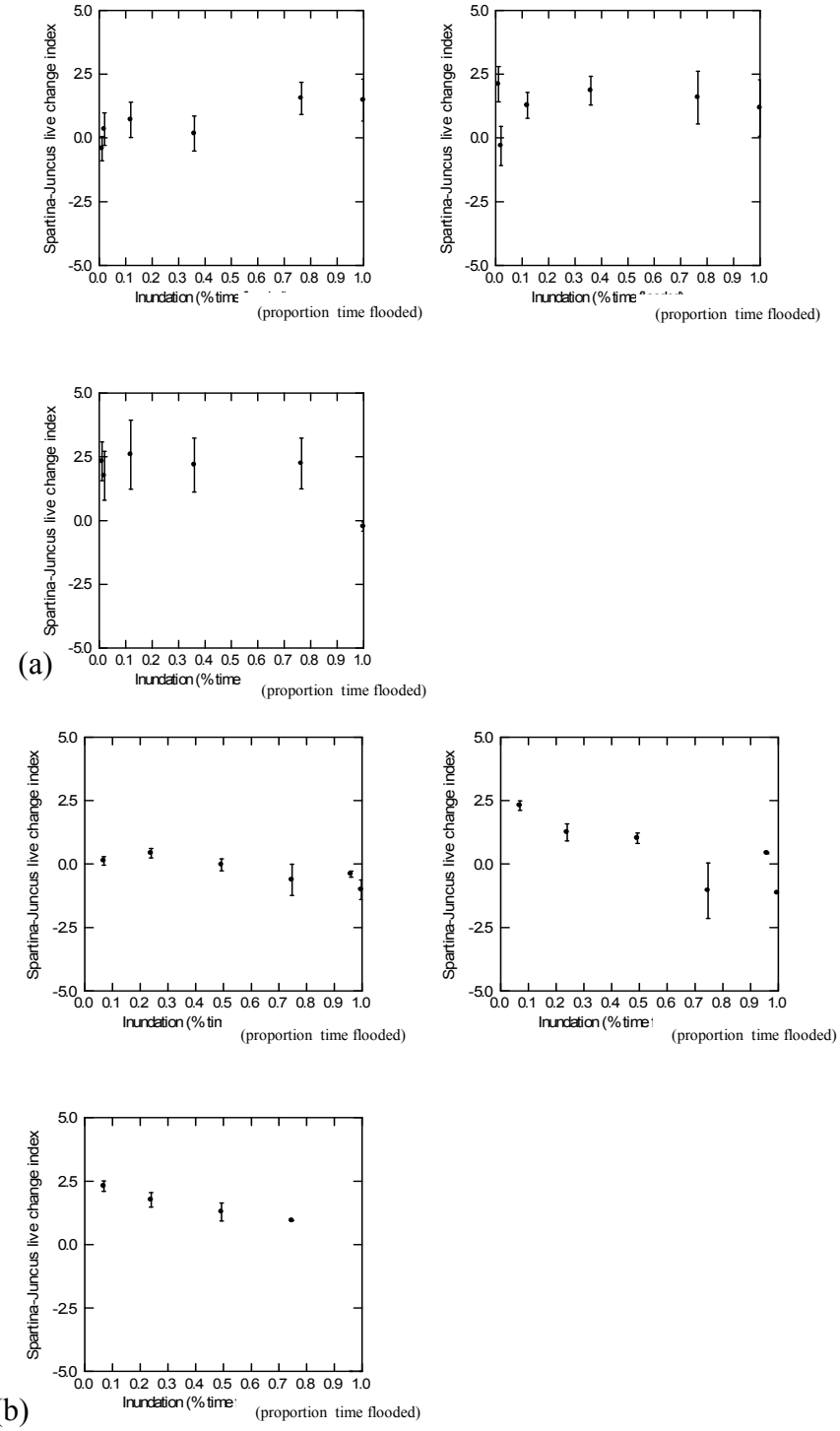

Figure 3.8. Indices of *Spartina* or *Juncus* dominance derived by subtracting the *Juncus* change in live length per pot by that of *Spartina* [(S live length chg) - (J live length chg)] / # days between sampling. April-June (upper left), June-July (upper right) and July-September (lower left) for (a) LOLA, (b) PKS and (c) REFERENCE planters

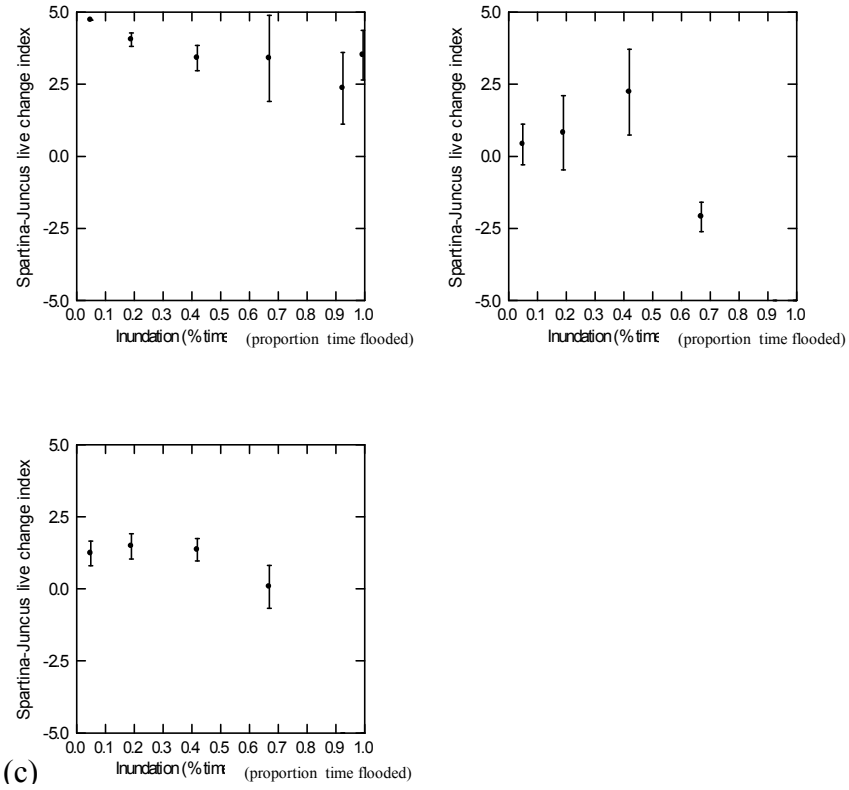

Figure 3.8. (cont'd) Indices of *Spartina* or *Juncus* dominance derived by subtracting the *Juncus* change in live length per pot by that of *Spartina* [(S live length chg) - (J live length chg)] / # days between sampling. April-June (upper left), June-July (upper right) and July-September (lower left) for (a) LOLA, (b) PKS and (c) REFERENCE planters (mean ± 1 SEM) Y axis index key: 0 = *Spartina* and *Juncus* contribute equally, greater *Spartina* contribution yields more positive values and greater *Juncus* contribution yields more negative values

The belowground material of the co-planted planters contained an intertwined mass of both *Juncus* and *Spartina* macro-organic matter. The EOS combined (both species) belowground biomass was inversely proportional to inundation at LOLA ($P<0.0001$); there was no trend in combined belowground biomass response to inundation at PKS (Figure 3.9). In an effort to detect differences in the belowground response of each species, the 3 longest roots of both *Spartina* and *Juncus* were measured for each co-planted pot. The only significant difference in this measure was observed at PKS, where the mean root length of *Spartina* was
inversely proportional to inundation period ($P=0.0001$) (Figure 3.10). The individually planted reference planter (PKS only) also yielded a trend of decreasing belowground biomass with increasing inundation for both species (Figure 3.9). However, as with the co-planted planter (root length only) from PKS, trend for root length was only significant for *Spartina* ($P= 0.0002$). In 2006, individually planted pots of *Spartina* and *Juncus* (at PKS) and *Juncus* (at LOLA) showed the same trend of decreasing belowground biomass with increasing inundation and this measure differed significantly ($P\leq 0.001$) in all planters.

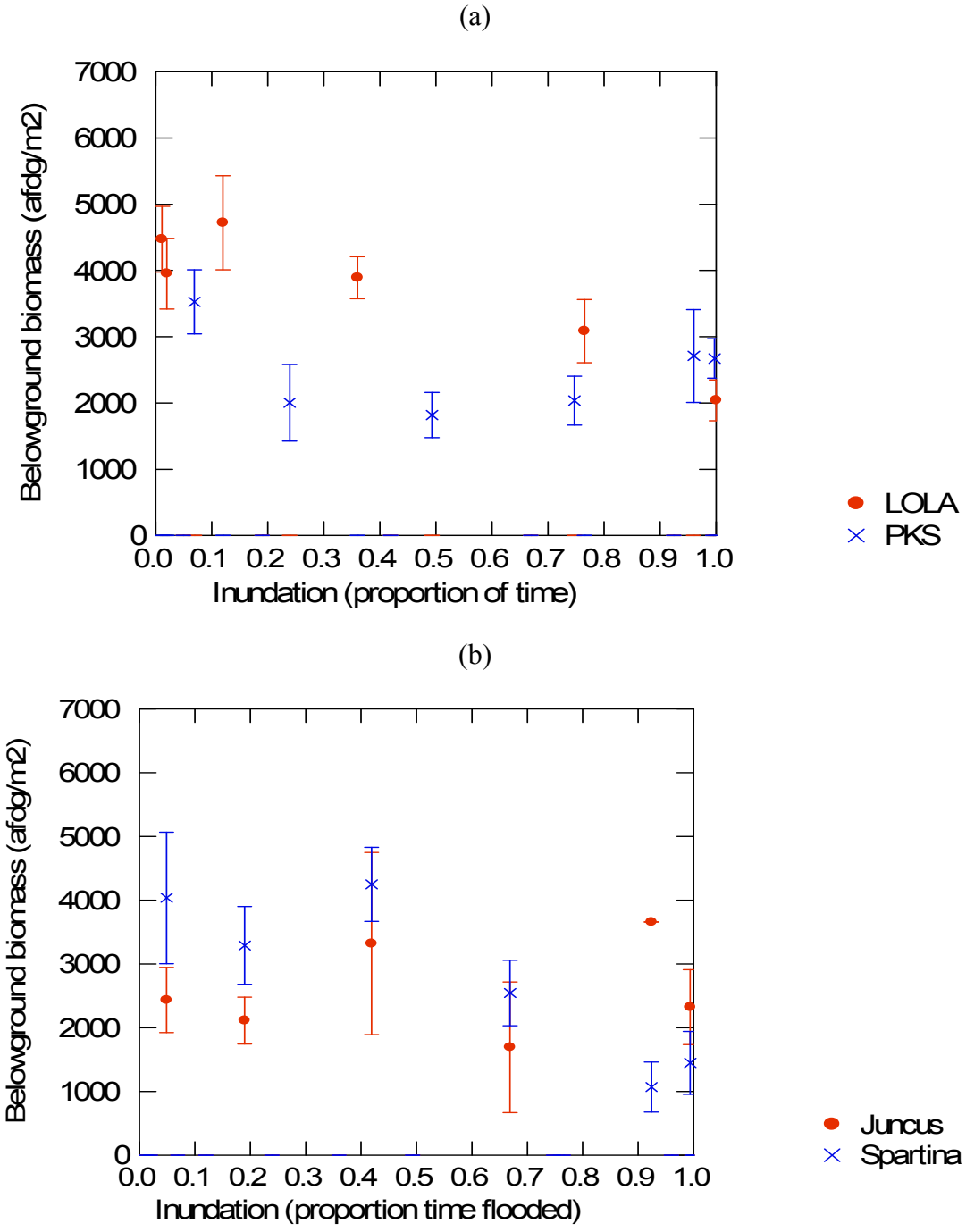

Figure 3.9. (a) Belowground biomass of planters co-planted with *Juncus* and *Spartina* at LOLA (red) and PKS (blue) and (b) Belowground biomass of reference planter containing individually planted *Juncus* (red) and *Spartina* (blue) Note: inundation is arcsine transformed for clarity

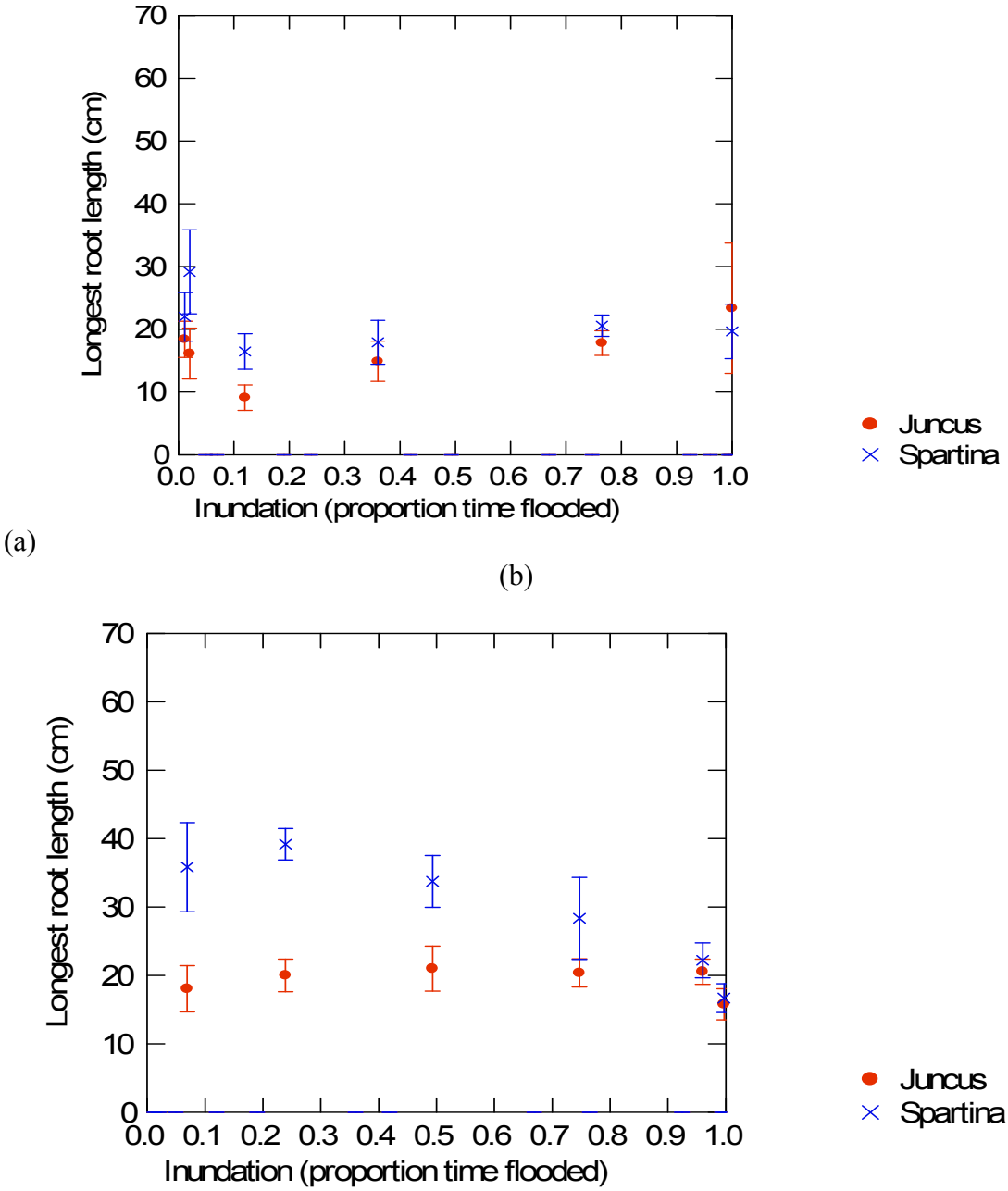

Figure 3.10. The mean of the 3 longest roots of *Juncus* (red) and *Spartina* (blue) in co-planted planters at (a) LOLA and (b) PKS

Platform disturbance plots

The experimental disturbance conducted along the *Spartina-Juncus* margin on the marsh platforms elicited a greater response from *Juncus* than from *Spartina* at both sites. Each plot consisted of a 1-m^2 quadrat of *Juncus* abutting a 1-m^2 of *Spartina*. The clipping disturbance significantly reduced the proportion of *Juncus* in respective quadrats at both PKS (P= 0.0002) and LOLA (P= 0.0477) when compared to controls, over 16 months (Table 3.2). In addition, the proportion of *Spartina* observed in *Juncus* quadrats was significantly greater in clipped plots at PKS (P< 0.0001) and LOLA (P= 0.009) than in controls (Figure 3.11). At PKS, a significant proportion of disturbed plots remained unvegetated in both *Juncus* (P=0.015) and *Spartina* (P=0.043) quadrats. Here, in October 2008, 19.3% (±8.38) of *Juncus* disturbed quadrats and 6.0% (± 7.12) of *Juncus* control quadrats contained bare cells; likewise, 6.3 % (±2.87) of *Spartina* disturbed quadrats and 5.5% (± 2.87) of *Spartina* control quadrats contained cells that were dominated by bare surface area. At both sites, variation within some treatments was sufficient to render differences between treatments as statistically insignificant; this was especially true for burnt plots at LOLA and for *Spartina* quadrats at PKS (Figure 3.11 and Table 3.2).

Table 3.2. Repeated measures analysis (P-values) of disturbance experiment at the *Juncus*-*Spartina* margin on marsh platform at PKS and LOLA, NC

		Juncus* in *Juncus	***Spartina* in *Spartina***	***Spartina* in *Juncus***	***Juncus* in *Spartina***	**Other spp. in *Juncus***	**Other spp. in *Spartina***	**Bare cells in *Juncus***	**Bare cells in *Spartina***
PKS									
between Tx		**0.0002**	0.3868	**<.0001**	0.4586	none	none	**0.0149**	**0.0431**
within Tx		**0.0030**	0.0908	**0.0006**	0.2501			0.1402	**0.0132**
Tx * Tx		**0.0017**	**0.0082**	**0.0004**	0.1464			0.1329	**0.0163**
LOLA									
between Tx		**0.0477**	0.7116	**0.0088**	0.6638	0.8796	0.5058	0.122	0.422
within Tx		**0.0162**	0.1492	0.0631	0.6721	0.1877	0.1273	**0.0001**	0.1117
Tx * Tx		**0.0205**	0.3317	**0.0400**	0.1808	0.5568	0.5731	**0.0002**	0.085
LOLA									
between Tx									
	Tx	**0.0365**	0.7141	**0.0075**	0.6774	0.3874	0.4988	0.0939	0.4302
	fire dist	**0.0564**	0.3880	0.1357	0.4105	**0.0358**	0.1743	0.0447	0.6787
	fire*Tx	0.9138	0.3286	0.3306	0.1818	0.2165	0.4870	0.7994	0.2502
within Tx									
	Tx	**0.0069**	0.1170	**0.0327**	0.7077	0.3380	0.1164	**<.0001**	0.0763
	Tx * Tx	0.0090	0.3036	**0.0181**	0.1805	0.3919	0.5979	**<.0001**	**0.0542**

Few additional species occurred at our research sites. I observed a greater variety of vegetative species at the LOLA site than at the PKS site; at LOLA, *Distichlis spicata* and *Salicornia* spp. were most prevalent among minor occurring species. No other vegetative species was observed in any experimental plots at PKS; however, *D. spicata* and *Salicornia* spp. were observed in the general study area. At LOLA, the percent cover of minor species was significantly (P= 0.036) greater in *Juncus* quadrats that had been disturbed by fire as compared to those not burnt for the entire study; the cover of these species did not vary (P= 0.39) between *Juncus* cut and control quadrats. At LOLA, minor species dominated cells in 0.75% (± 1.5) and 2.0% (±1.83) of control and cut plots, respectively, within both species in the burnt area. And minor species only dominated cells in 0% and 0.75 (±1.5) of control and cut plots, respectively, within both species in the unburnt area. Sixteen months after the cutting disturbance, there were actually more cells consisting of minor species in *Spartina* than in *Juncus* burnt quadrats, in both cut and control plots. However, the burning factor was not significant (P= 0.174) overall for the presence of minor species in *Spartina* quadrats. Plant communities within the areas previously exposed to fire were more diverse than unburnt areas in both control and cut plots (Figure 3.11). Within the first 16 months (2 growing seasons) of this experiment, *Juncus* exhibited depressed resilience to a pulsed disturbance, and *Spartina* has shown competitive dominance over *Juncus* at both sites following a pulsed disturbance.

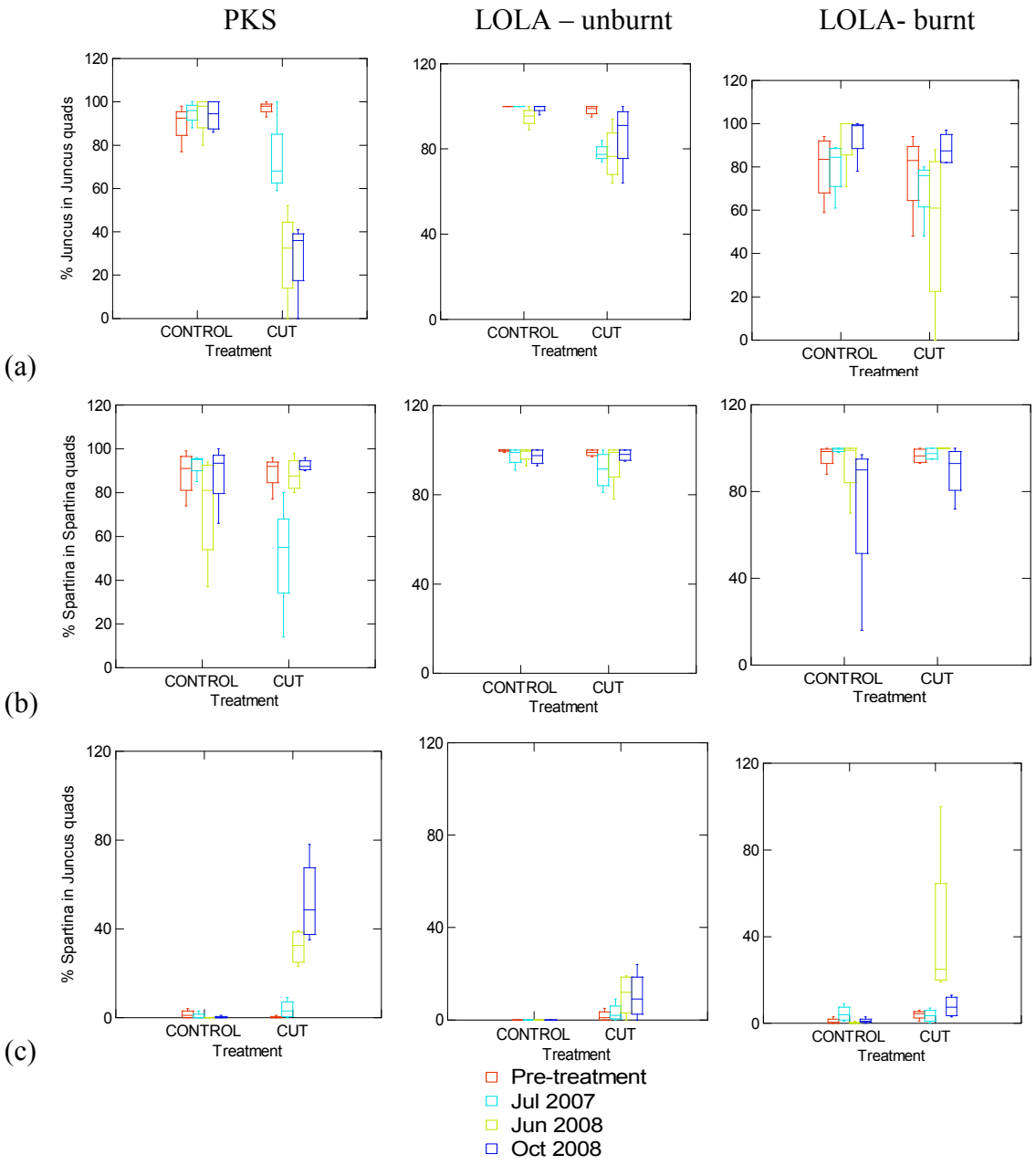

Figure 3.11. Proportions of (a) *Juncus* in *Juncus* quadrats, (b) *Spartina* in *Spartina* quadrats, (c) *Spartina* in *Juncus* quadrats, (cont'd...) in control and cut plots at PKS (left column), LOLA unburnt zone (center column) and LOLA brunt zone (right column) prior to treatment (0 mo.), July 2007 (2 mo.), June (12 mo.) and October (16 mo.) 2008

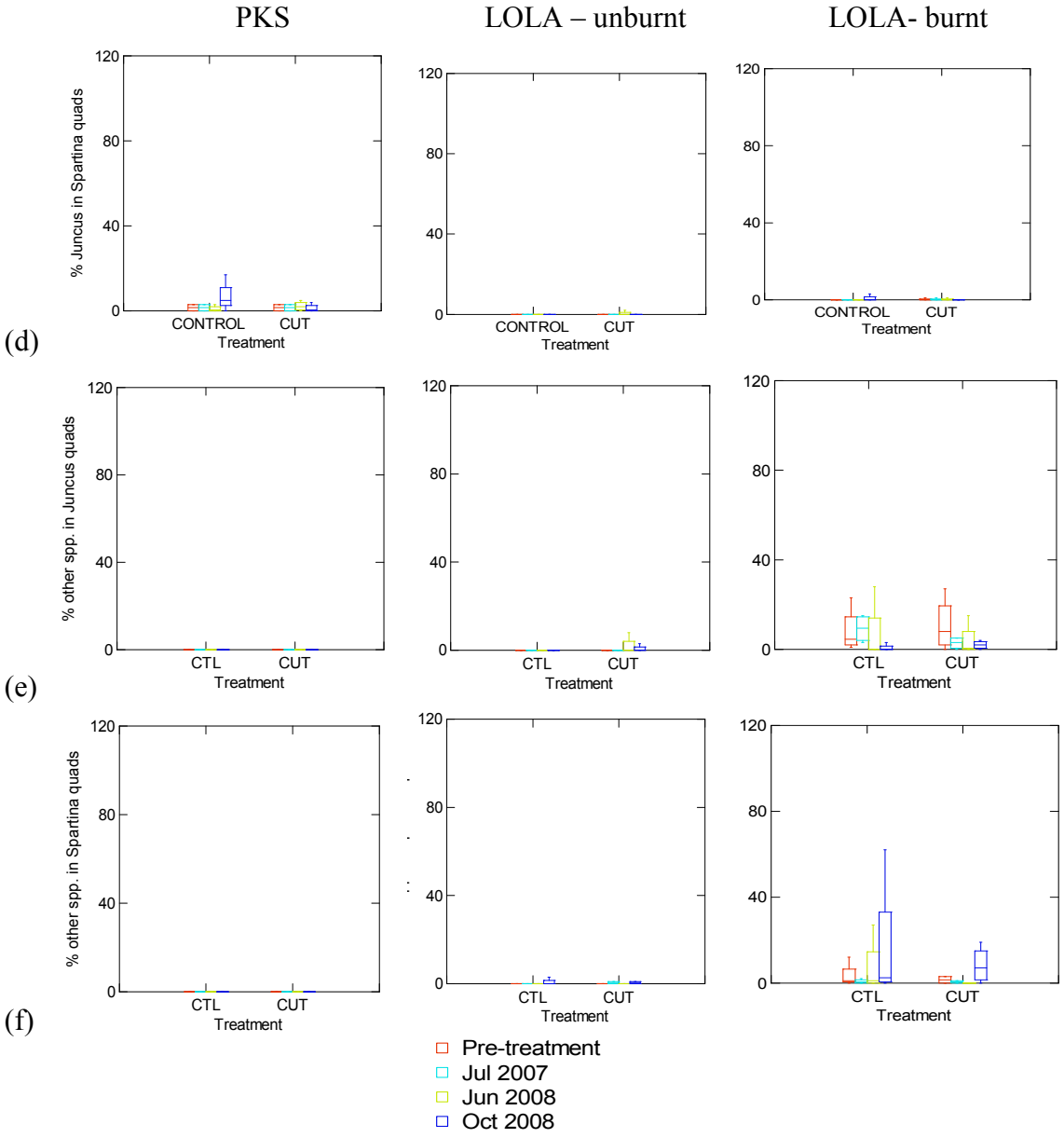

Figure 3.11. Proportions of (...cont'd) (d) *Juncus* in *Spartina* quadrats, (e) other species in *Juncus* quadrats, (f) other species in *Spartina* quadrats (...cont'd) in control and cut plots at PKS (left column), LOLA unburnt zone (center column) and LOLA brunt zone (right column) prior to treatment (0 mo.), July 2007 (2 mo.), June (12 mo.) and October (16 mo.) 2008

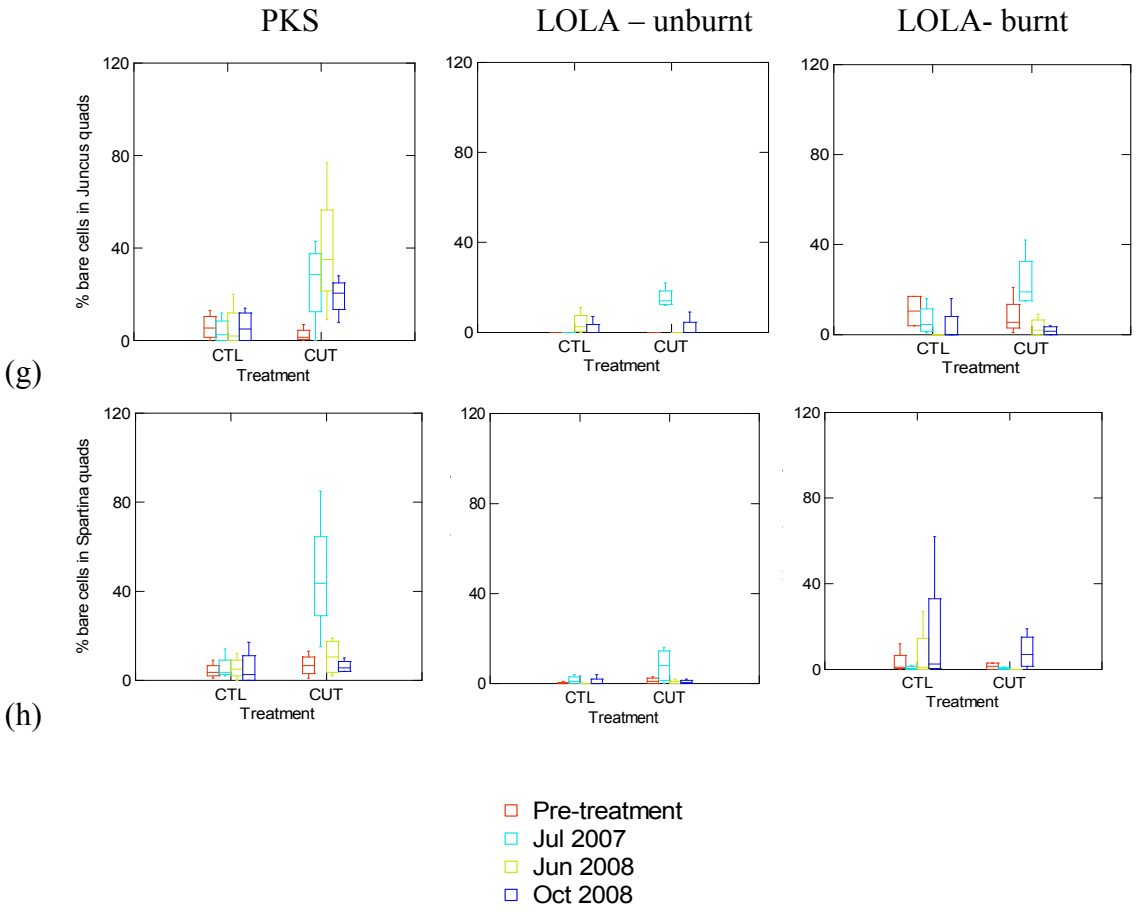

Figure 3.11. Proportions of (...cont'd) (g) bare cells in *Juncus* quadrats and (h) bare cells in *Spartina* quadrats in control and cut plots at PKS (left column), LOLA unburnt zone (center column) and LOLA brunt zone (right column) prior to treatment (0 mo.), July 2007 (2 mo.), June (12 mo.) and October (16 mo.) 2008

Discussion

In this study, the response of *Juncus* and *Spartina* was evaluated when cultivated jointly over a range of inundation periods. Little difference was found between the net growth responses of these dominant macrophyte species. In mesocosms, EOS aboveground biomass of both species was inversely related to inundation period with no species interaction. Seasonal production of both *Spartina* and *Juncus* were greater within an irregularly inundated regime (LOLA) where salinities were slightly lower and wind-driven wave action was less than in the semi-diurnal inundation regime (PKS). In a separate experiment on the marsh platform at the same sites, the percent cover of *Juncus* yielded significantly to *Spartina* for at least 16 months following a pulsed disturbance where these species are naturally delineated. Data revealed no significant interaction between *Spartina* and *Juncus* with inundation period and a significant decline in *Juncus* and encroachment of *Spartina* after a pulsed disturbance event.

Trends of decreasing EOS aboveground biomass with increasing inundation were similar to those of *Spartina* and *Juncus* grown over a range of inundation periods in individual planter pots at PKS (in 2006 & 2007) and likewise for *Juncus* only at LOLA (in 2006) (chapter 2, this dissertation). Overall, the co-planted and reference planters at PKS exhibited signs of greater stress (poor growth) than did the co-planted planter at LOLA in 2007 and compared to the three planter experiments at both sites in 2006.

In multi-level marsh planters, *Spartina* was found to be slightly dominant in relative net seasonal production over *Juncus* (Figure 3.6). The dominance by *Spartina* was inversely proportional to inundation in a semi-diurnal inundation regime and without

trend in an irregular inundation regime (Figures 3.6 and 3.8). At LOLA, the irregularly inundated site, *Juncus* exhibited a threshold effect showing a sharp decrease in production when inundated ≥ 77% and likewise for *Spartina* when inundated 100 % (Figures 3.4 and 3.5). While the proportion of live *Spartina* increased more than that of *Juncus* in a majority of inundation treatments, the cause of greater senescence by *Juncus* remains unclear. Results support the findings of Eleuterius and Eleuterius (1979) in their determination that inundation period did not explain the sharp delineation between *Spartina* and *Juncus* zonation. The inundation tolerance ranges of *Spartina* and *Juncus* overlap greatly, yet *Spartina* does withstand a greater degree of inundation than does *Juncus* (Pennings et al. 2005, chapter 2, this dissertation). Pennings et al. (2005) found that *Spartina* better tolerated inundation than did *Juncus* in transplant experiments. In mesocosm experiments, Voss et al. (chapter 2, this dissertation) found that *Spartina* yielded more net growth over a greater range of inundation than did *Juncus*, with growth essentially ceasing at inundation periods ≥ 67 % and ≥ 42 to 53 % for *Spartina* and *Juncus*, respectively. In this mesocosm experiment (which examined 6 inundation treatments over a range from 1.1 to 100% inundation periods), macrophyte dominance sometimes differed significantly by inundation period, yet trends in *Spartina* dominance in co-planted mesocosms were weak and differed by inundation regime (Figures 3.6 and 3.8). Hence, the general uniformity of *Spartina* dominance across inundation periods may be due to its broader tolerance to inundation over *Juncus*.

The generally greater relative aboveground contribution by *Spartina* over *Juncus* may have been influenced by macrophyte growth patterns as well. Christian et al. (1991)

and Williams and Murdoch (1972) found that new *Juncus* leaves grow (increase in green length) during the months of March through early August and subsequently senesce (die back from tip to leaf base) from mid-August until complete death (100% brown) about one year later. *Juncus* leaf growth may continue from the basal meristem while senescence proceeds from the leaf tip (Christian et al. 1991). In South Carolina, Morris and Haskin (1995) found *Spartina*'s maximum monthly growth rates to occur during the months of July and August and peak biomass density occurred in September. The dominance indices that rely heavily upon September EOS data (Equations 1 and 2) may reflect the natural late-season senescence of *Juncus*, which co-occurs during peak *Spartina* productivity. The black needle rush, *Juncus*, grows more slowly and persistently throughout the year (Eleuterius 1975, Christian et al. 1990), while the grass, *Spartina*, becomes dormant in the winter with active growth occurring in warm months (Teal and Kanwisher 1966, Turner 1976, Mendelssohn and Morris 2000). The growth characteristics of the two macrophytes examined vary in their annual life cycle. Therefore, the use of end-of growing-season metrics to assess production may yield a more accurate interpretation of *Spartina* net production than it does for *Juncus* production. The EOS biomass density assessment is the standard in the field of marsh ecology (Hopkinson et al. 1980), because a majority of coastal marsh research has traditionally focused on *Spartina*.

This study found no interaction between *Spartina* and *Juncus* growth patterns and inundation period, yet response to disturbance differed by species. Pennings et al. (2005) found that *Juncus*: (1) reduced *Spartina* biomass in low salinity (10 psu) treatments that

received a regular flooding and draining sequence and (2) increased *Spartina* biomass in low salinity treatments that remained flooded. These authors propose that *Juncus* might facilitate *Spartina* by oxygenating soils. My planter results do not illustrate a competitive or a facultative relationship between *Spartina* and *Juncus* with inundation period or regime. However, co-planted pots were generally more productive than individually planted pots at the site where this comparison was possible (PKS). At LOLA, the net growth of *Juncus* was similar between the co-planted pots (2007) and individually planted pots (2006). On the marsh platform, I observed greater resilience in *Spartina* plots than in *Juncus* plots to a cutting disturbance at both sites. Observations also revealed a significant invasion of *Spartina* in disturbed *Juncus* plots at PKS ($P< 0.001$) and LOLA ($P=0.009$).

Inundation regime was an important factor in the net production of both *Spartina* and *Juncus*. The seasonal change in aboveground biomass was significantly lower in co-planted mesocosms cultivated at PKS than that cultivated at LOLA. However, the species dominance indices did not differ with inundation regime. The growth patterns of *Spartina* and *Juncus* differed by regime, yet their response to inundation period was similar. The reduced EOS live *Juncus* in the astronomically-dominated regime revealed a significant ($P= 0.003$) interaction with inundation period. Wind-driven wave energy was an obvious abiotic variable that differed between the two inundation regimes that could explain differences in net production at my sites. Fetch length can be used as a proxy for wave energy. The PKS site had a fetch length 30 times greater than that of LOLA and therefore was assumed to have experienced a higher energy regime. Fetch length for the

mesocosms was approximately 3 km and 0.1 km at PKS and LOLA, respectively. Even though marshes at the southern end of the Pamlico Sound can experience a fetch length of up to 100 km, the research site, at LOLA, was positioned within a confined lagoonal area. The PKS site was protected to some extent; however, it experienced the greatest fetch from northerly winds, which dominate in storm conditions and tend to occur at relatively higher wind speeds. An estimate of wave climate along a shoreline can be made by considering fetch distance, wind speed, wind direction and percentage of wind occurrence; these are the components of the Relative Exposure Index (REI) developed by Keddy (1982) and further modified by Shafer and Streever (2000). Sites with higher REI values experience greater wave energy. Cowart et al. (2007) calculated the shoreline REI at the LOLA site to be approximately 12; this was much lower than the mean REI for the PKS area that was estimated to be 66 (range: 25 - 167). Here, the specific mesocosm site was only analyzed for LOLA. Marsh planter mesocosms were positioned to reflect the environmental conditions experienced by a majority of marsh habitat within respective regimes.

The estuarine salinity was comparable between the two inundation regimes. Even though estuarine salinities were similar and often overlapped, the two sites were classified differently in terms of salinity, with the PKS site (34 ±1.8 psu) being euhaline and the LOLA site (29 ±4.3 psu) being polyhaline. Because I did not manipulate this variable, nor did it differ significantly between sites, my data do not allow me to draw a conclusion about the effect of salinity on the interaction of *Spartina* and *Juncus*.

Pulse and repeated press disturbances appear to play a key role in shaping community structure within marsh habitat. An experimental pulsed disturbance (cutting) elicited community shifts in experimental plots established along the *Juncus* and *Spartina* margin on marsh platforms. Within both inundation regimes, *Juncus* cover was significantly reduced with significant *Spartina* encroachment in response to cutting compared to controls. These findings concur with the paradigm noted in the introduction. *Juncus* is considered competitively superior to *Spartina* (Pennings et al. 2005); it therefore occupies the least stressful zones, thus displacing competitively inferior species (here, *Spartina*) to more stressful zones (Bertness 1991, Bertness 1992, Pennings and Bertness 2001, Pennings et al. 2005). Disturbance may explain the community shift that was observed at the naturally occurring margin of these macrophytes. Additional observations from this study support this paradigm, as well as demonstrate the effects of pulse (cutting) and repeated press (wave energy) disturbances. At the more energetic site (PKS), a significant proportion of surface area remained bare after disturbance in plots of both species, underscoring the stressful conditions in which no macrophyte colonized. At this site, I hypothesize that relatively higher wave energy was also responsible for the decreased net production observed in the mesocosms experiments. Wave energy is such an important stressor here that it may be largely responsible for the zonation of macrophytes rather than inundation alone. Only *Spartina* occupies the marsh intertidal zone within 10 m from the estuarine edge at PKS, although areas that are more distal are regularly inundated. Both *Juncus* and *Spartina* occur in a mosaic of monotypic patches for a broad zone, landward of the 10 m edge zone, where wave energy has been reduced.

At the more quiescent site (LOLA), both *Juncus* and *Spartina* occur along the estuarine edge of marshes, as well as in random monotypic patches across the marsh. In addition, other competitively inferior (Bertness 1991) species (e.g., *D. spicata* and *Salicornia spp.)*, species typically associated with high marsh, were observed across the LOLA marsh, indicating perhaps that wave-action disturbance was insufficient to exclude these species. These infrequently occurring species were present at relatively higher densities in both control and cut plots that had been disturbed by fire prior to the initiation of the disturbance experiment, indicating that a burning disturbance elicited a community shift. While this study was not designed to quantify wave energy, sufficient evidence exists to consider future research on the relative impacts of wave energy and inundation period on *Juncus* production.

Collectively, these observations suggest that the cumulative effects of multiple disturbances (e.g., fire, wrack deposition, wave action and inundation) may be greater than that of individual disturbances (Sousa 1984, Turner et al. 2003). Based on this study and the work of others, it has been postulated that pulsed (cutting, wrack deposition) and repeated press (wave energy) disturbances yield a more pronounced response than do press disturbances (SLR) (Sousa 1984, Turner 1989, Turner et al. 1993). Tolley and Christian (1999) found the effect of a pulsed wrack deposition disturbance to override the effects the press disturbance of increased inundation in an experiment designed to separately quantify both disturbance types. Understanding the role of disturbance type, frequency and severity, as well as that of cumulative effects, is an area of research requiring more attention given the anticipated impacts of global climate change. The

findings of this study support the conceptual model of ecosystem state change proposed by Brinson et al. (1995) in which the effects of a press disturbance (e.g., sea-level rise) may be less evident than the effects of pulsed (e.g., wrack deposition, fire) or repeated press (wave action) disturbances, which may push an ecosystem state beyond a threshold from which it can recover. However, it is the press disturbance that moves the threshold closer to the tipping point and the pulse/repeated press disturbance that ultimately results in a change of ecosystem state (Brinson et al. 1995, Christian et al. 2000).

Ecosystem disturbances can be viewed as events or processes that reset the successional 'clock' (Sousa 1984, Turner et al. 2003). Such perturbations test ecosystem resiliency and may even increase resiliency by increasing biodiversity (Southwood 1977, Sousa 1984, Mooney and Godron 1983, Peterson 1997). As the effects of multiple disturbances (presses and pulses) accumulate and interact, ecosystem resilience is likely to decrease (Turner 1993, Folke et al. 2004). Sea-level rise is a press disturbance (e.g., increased inundation and wave action) that continually shifts the tolerance range of organisms in a landward direction. Under a scenario of accelerating SLR, organisms may be displaced further landward with each pulsed disturbance event (e.g., storm, fire, wrack deposition). Cumulative disturbances may serve as a mechanism that drives the transgression process on a landscape scale.

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Chapter 4. MEASURING THE LOSS AND RESTORATION OF COASTAL MARSH ECOSYSTEM SERVICES

Abstract

Marsh ecosystems are recognized for providing a wealth of ecosystem services within the world's coastal zones. The contributions of these services are often not fully recognized until ecosystem function is reduced or eliminated. In the U.S.A., the Clean Water Act, Comprehensive Environmental Response, Compensation, and Liability Act (CERCLA), the Oil Protection Act and the Coastal Zone Management Act (in part) have been enacted in an attempt to sustain the societal benefits derived from such public trust resources. A key challenge to those responsible for the management of public trust resources is the qualification and quantification of the ecosystem services provided by natural resources. In this chapter, I critically review the scaling of the losses and gains in marsh ecosystem services within the context of coastal marsh habitat injury, restoration and creation as achieved by the Natural Resource Damage Assessment (NRDA) process. I focus on the methods and criteria used for compensatory restoration measures. The "scaling" of ecosystem services is a method for quantifying ecosystem services and has been used historically in NRDA and compensatory restoration cases. This method involves: (1) the identification of natural resource ecosystem services, (2) the selection of metrics for ecosystem services which serve as a proxy for ecosystem function and condition, (3) the quantification of service using those proxies and (4) development of equivalency models that demonstrate how alternative restoration projects offset ecosystem losses. Here, I discuss the use and determination of metrics (or suites of metrics) that effectively, efficiently and defensibly evaluate the ecosystem services of

natural, injured and restored marshes. After an introduction of compensatory restoration, Habitat Equivalency Analysis and marsh ecosystem services, I discuss: (1) quantification of marsh injury, (2) quantification of marsh creation and restoration, (3) insights from the hydrogeomorphic approach and (4) climate change considerations for restoration projects.

Introduction

Context for measuring ecosystem services

Natural ecosystems provide a suite of ecosystem services that sustain the functioning of the ecosystems themselves and enrich human experience, enterprise, and endeavor (Daily et al. 1997, CESR 2008). For example, as part of a co-evolutionary partnership honeybees pollinate many terrestrial plants, facilitating their propagation, while also serving to pollinate the flowers of orchard trees and field crops essential to agricultural production. The contributions from ecosystem services are often unrecognized, unappreciated and undervalued. As a consequence, environmental insults to public and private waters and lands and the ecosystems they support were long accepted without requiring compensation. Oil spills, chemical releases, habitat destruction during land development, and many other human-induced perturbations to natural ecosystems represented an externalization of the cost of doing business, with the public rights implicitly being transferred to private rights when degraded services were not replaced by the parties responsible.

In the United States, numerous federal policies and legislative acts have recognized the consequence of preserving critical ecosystem services provided by public trust resources and have established requirements for the compensation of environmental injuries. A "no net loss" policy for wetlands under the federal Clean Water Act requires that construction projects avoid, then minimize where unavoidable, and finally mitigate any remaining damage to wetlands. The Comprehensive Environmental Response, Compensation, and Liability Act (CERCLA) and the Oil Pollution Act (OPA) establish

procedures for federal and state governments and American Indian tribes to assess injuries to natural resources caused by oil or chemical releases and to seek compensatory restoration for losses to the public trust system. The authority to seek compensation for natural resource damages (NRD) under these statutes has led to a burgeoning field of study. Other United States laws with a restoration component include the Coastal Zone Management Act, the Endangered Species Act, the Marine Mammal Protection Act and others (Allen et al. 2005). Requirements for restoration and public compensation for resource injuries have more recently been adopted in the European Union under the Environmental Liability Directive of 2004 (EU 2004).

In this chapter, I use the framework established by U.S. statutes and the natural resource damage assessment (NRDA) process as a basis for qualifying and quantifying the ecosystem services rendered by coastal marsh habitat. In an effort to assure that services rendered by public trust resources are sustained, trustees must determine ways in which injury to and restoration of ecosystem services can be measured and balanced. This is achieved by itemizing: (1) the level of damage to a given natural resource, (2) a prediction of the level of natural or aided recovery of ecosystem services (primary restoration), (3) interim losses in services and (4) appropriate secondary restoration alternatives to compensate for interim losses (compensatory restoration). Primary restoration involves returning resources to their baseline condition. Compensatory restoration involves a series of steps, beginning with identification of the ecosystem services that are affected, then progressing to selection of proxies (metrics) representing the most important ecosystem services, quantification of injury using those proxies, and

development of equivalency models that demonstrate how alternative restoration projects offset ecosystem losses. Such techniques collectively determine the appropriate scale of compensatory restoration actions and are often known as "restoration scaling" methods (NOAA 1997, Chapman and Julius 2005).

Figure 4.1 shows graphically the role of compensatory restoration in offsetting lost resource services. When an incident occurs that causes resource injury, services decline to below their baseline level. "Baseline" refers to the level of services the resource would have provided through time had the injury not occurred. The baseline level of services varies over time and thus is not necessarily the same as the level of services prior to injury because of temporal variations in natural environmental forcing factors and other human interventions impacting resource services. Efforts may be undertaken to minimize the further spread of or directly remediate the resource injury, and these efforts are often termed "primary" restoration. Primary restoration accelerates recovery to baseline, reduces the total quantity of services lost over time, and reduces the required quantity of compensatory restoration. Area A under the baseline services curve in Figure 4.1 shows the total loss in services that accrues prior to recovery, sometimes described as "interim" loss. Note that this interim loss would have been greater in the absence of the primary restoration done to contain the damage. Restoration scaling methods determine appropriate compensation by establishing equivalence between services lost in area A and services gained in area B.

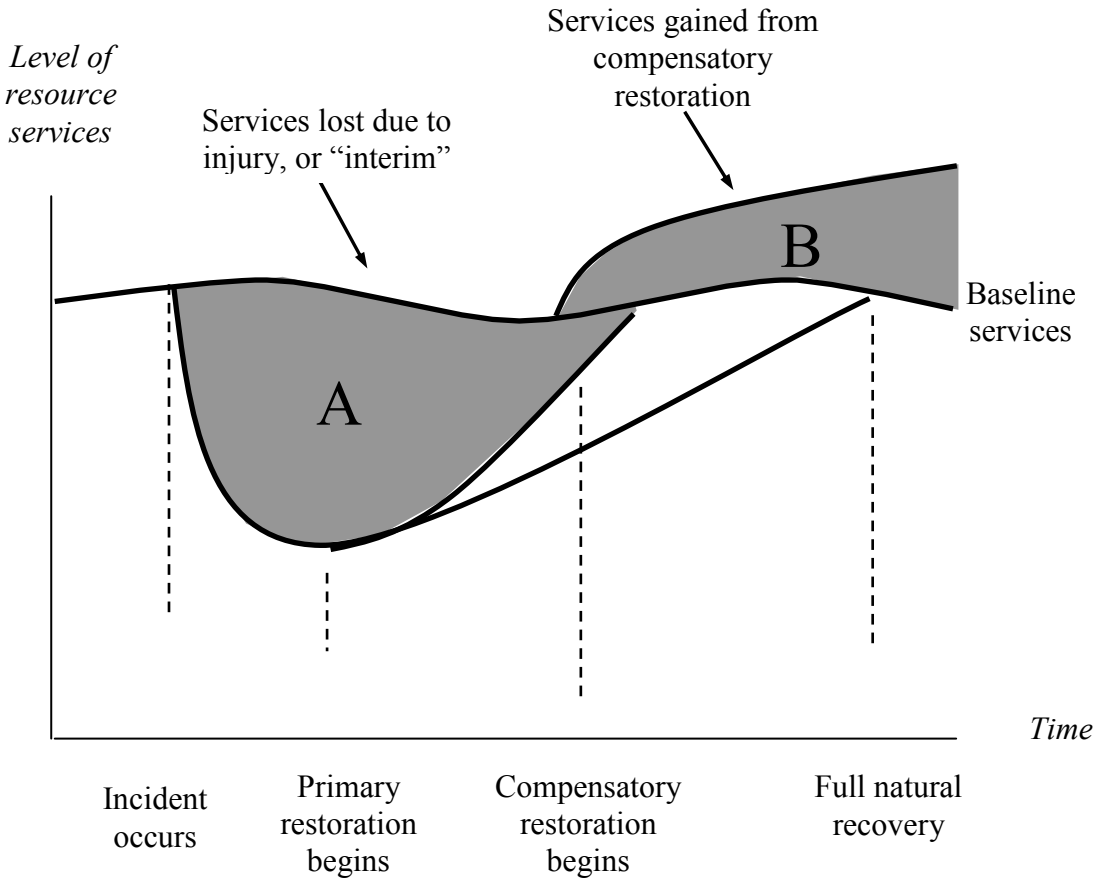

Figure 4.1. Using compensatory restoration to offset lost resource services (English et al. 2009)

Compensatory restoration projects are selected and compensatory restoration is implemented at some time following the initial incident. Some resource types are restored, established or enhanced with the purpose of providing compensation for future or unavoidable resource damages, such as with wetland mitigation banking (USFWS 1983, NAS 2001). Compensatory restoration increases resource services to above their baseline level and thereby holds potential for offsetting the interim losses (Figure 4.1). Compensatory restoration is distinguished from primary restoration in that it enhances or replaces services different from those injured, with the difference being either the type of services restored or the location where services are restored. Baseline services are conveyed with respect to restoration are thus distinct from the injury baseline, but are illustrated in the graph using a single line for simplicity. The difference between restored and baseline services for compensatory projects traces out area B, representing the total gains from compensatory restoration over time.

Habitat equivalency analysis (HEA)

Compensation for interim losses had been traditionally viewed as a claim for monetary damages (Yang et al. 1984, DOI 1986). With the recovery of injured resources addressed through primary restoration, the motivation for addressing interim losses was primarily economic, involving compensation, incentives to deter polluting activities, and fairness. The need to address interim losses is particularly clear when the best course of action at an affected site is to allow for natural recovery; compensating for interim losses yields no net loss of resource benefit, in theory (Brans 2001). A practical solution was to calculate the value of interim losses and spend the recovered funds on resource

enhancements. Difficulties with this approach included the high cost of studies to value resource injury and controversies surrounding the available economic methods, such as contingent valuation (Arrow et al. 1993).

Recognizing the high cost of resource valuation studies, Unsworth and Bishop (1994) proposed Habitat Equivalency Analysis (HEA) as an alternative approach to determining compensation for interim losses. Their published article formalizes methods that practitioners in the field had been developing over several years. Habitat Equivalency Analysis relies on metrics such as vegetative cover or sediment toxicity to evaluate a change in habitat ecosystem services. The HEA model that they developed involves a set of economic assumptions that allows monetary values to be replaced by units of habitat area. The emphasis shifted from a damages-based claim to a compensation-based claim, with losses in habitat area replaced by gains in habitat area. The amount of a claim for compensation is then based on the cost of restoring the required habitat area, and the exercise of converting habitat losses to a monetary value is no longer necessary. The HEA method was upheld in court in *United States v. Fisher* (1997) and *United States v. Great Lakes Dredge and Dock* (2001).

Subsequent studies refined the HEA model and replaced simple measures of habitat area with more precise biological metrics of habitat service and function (Fonseca et al. 2000, Strange et al. 2002, Cacela et al. 2005). The expanded set of metrics measures biological changes that are assumed to be directly proportional to changes in public value, so that the exercise of monetizing value can be avoided. In 1996, regulations for the Oil Pollution Act expressed an explicit preference for HEA models over monetary

valuation (NOAA 1996). However, more recent regulations issued under the Superfund law (CERCLA) refrained from affirmatively encouraging HEA over methods based on monetary valuation (DOI 2008). Methods for quantifying service losses induced by injury and service gains emerging from restoration require the development of an appropriate metric or suite. Like most modeling techniques, the selection of a metric involves a tradeoff between simplicity and realism. A metric must be simple enough to be observed with reasonable precision and at reasonable cost. However, selection of a simple metric limits consideration of multiple complex factors relevant to the realistic evaluation of ecological services. There are situations in which employing a suite of metrics is more effective in defining a level of ecosystem service; however, in reality, one must balance the effectiveness of using multiple metrics with efficiency.

Units used in metric-based scaling incorporate the basic elements of ecosystem service losses and gains over time. All units are discounted, services are frequently quantified by habitat area (often acres), and the time periods are frequently expressed as years. This leads to the use of discounted service-acre-years (DSAYs) as the most common scaling unit. One DSAY of salt marsh habitat is equal to the value of services provided by one acre of salt marsh in year 0. The value of one acre of salt marsh provided at some later date has a year - 0 equivalent that is less than one DSAY due to the effect of discounting. Discounting accounts for the public preference of immediate service over delayed provision; hence, it reduces the measured importance of future benefits. In other words, there is a higher value given to one acre of fully-functional marsh today than at ten years in the future. Sometimes habitat services are measured not

as the presence or absence of habitat, but as changes in the level of habitat function. For example, if a restoration project increases services in one acre of marsh from a level that is 50% of full function to a level that is 80% of full function in a given year, then the annual value of restored service flows is 0.3 service-acre-years.

Measuring ecosystem services of coastal marsh habitat

Coastal marshes have been acknowledged as being among the most highly-valued (per hectare) of Earth's ecosystems (Costanza et al. 1997) because their structure and function provide essential ecosystem services. They are also among the most vulnerable of ecosystems, positioned at the interface between the terrestrial and aquatic realms, exposing them to terrestrial run-off high in nutrients, sediments, and contaminants as well as aquatic pollutants. Generally, this habitat is highly productive per unit area, yet threatened by land development pressure and habitat alteration and is vulnerable to deposition of floating pollutants such as oil. Coastal marshes of the continental U.S. differ regionally as a function of variations in coastal tidal hydrology, geomorphology, human encroachment, and biotic province. The most extensive marshes occur along the Gulf of Mexico coast, especially in Louisiana and Florida, and along the Middle and South Atlantic coast; the less extensive are along the North Atlantic coast, and marsh acreage per unit of ocean shoreline is lowest on the Pacific coast, particularly in Central to Southern California (NOAA 1990). Whereas the highest percentage loss (90%) of historic coastal wetlands has occurred in California (NOAA 1990), the greatest losses in marsh area have occurred in Louisiana and Florida (Dahl 1990).

Marsh ecosystems are unique in their structure, function and in their contribution of services for which few or no alternatives exist. Marsh plant communities are low in species diversity and the typically few dominant species tend to be notably stress tolerant (Stout 1984, Bertness and Ellison 1987, Mitsch and Gosselink 2000, Sullivan and Currin 2000). North America as a whole is exceptional for the large number of terrestrial vertebrate taxa that are endemic or largely restricted to tidal marshes (Greenberg et al. 2006). Because of often differences in elevation and subsequent flooding frequency and duration, tidal marshes exhibit substantial spatial heterogeneity in ecosystem services. Ecosystem services of coastal marshes include the following: (1) high productivity and habitat provision supporting the foodweb leading to fish and wildlife (Teal 1962, Weisberg and Lotrich 1982, Boesch and Turner 1984, Peterson and Turner 1994, Minello et al. 2003), (2) buffer against storm wave damage (Mitsch and Gosselink 2000), (3) shoreline stabilization (NCDCM 2006), (4) flood water storage (Mitsch and Gosselink 2000), (5) water quality maintenance (Stone et al. 1990, Correll et al. 1992), (6) biodiversity preservation (Keer and Zedler 2002; Callaway et al. 2003), (7) carbon storage and biogeochemical cycling (Mitsch and Gosselink 2000, Chmura et al. 2003, Brevik and Homburg 2004, Choi and Wang 2004) and (8) socio-economic benefits (Mitsch and Gosselink 2000, MEA 2005).

Quantifying ecosystem service loss to marsh injury

Here, I review two case studies and primary literature findings of valuation methods for quantifying habitat injury and restoration. These methods have already met ecological and legal criteria for being effective, efficient and defensible. The Chalk Point case (NOAA et al. 2002) best represents the current HEA method for quantifying injury in forms appropriate for scaling compensatory restoration of marsh habitat. The Bailey Trustee Council (2003) case offers insight into how to treat different marsh habitat types and associated non-marsh habitat for the purposes of quantifying restoration. Subsequently, I consider what metrics best represent the suite of ecosystem services provided by marsh habitat, looking ahead to where injury assessment may progress in the future.

Applying HEA: the Chalk Point case

The Chalk Point oil spill case illustrates well the current HEA method for quantifying coastal marsh injury. Both marsh vegetation and soil condition were used as metrics to capture two categories of ecosystem services provided by marsh habitat and to determine degree of injury caused by an oil spill. Aboveground marsh biomass and density reflect a wide range of ecological functions related to primary production, trophic support, habitat structure, fish and shellfish production, as well as recreational and aesthetic value (Peterson et al. 2008a). Marsh soils are important for habitat for invertebrates, long-term support of marsh plants, and biogeochemical cycling and/ here, allows the quantitative measure of a chronic toxic-oil substance. In this case, injuries to about 76 acres of brackish marsh, as well as other connected estuarine habitats, resulted

from a spill of No. 2 and No. 6 fuel oil from a ruptured underground pipe in the marsh along Swanson Creek, on the shore of Chesapeake Bay, Maryland (NOAA et al. 2002). Field surveys along with aerial photography of the marsh demonstrated that 23.4 acres were heavily oiled, 12.0 acres moderately oiled and 40.5 acres lightly oiled. Surveys were conducted immediately after the April 2000 spill, then in July and September, and again in July 2001. These provided data on the oiled appearance on the soil surface, vegetation, and subsurface of the soil. Several metrics were established from samples taken within 61 1-m^2 quadrats in both oiled and reference areas. These include: (1) the degree of oiling (coverage and thickness), (2) vegetative metrics of marsh grasses (stem height and density, percent cover), (3) sediment chemistry (marsh surface soils evaluated for levels of total petroleum hydrocarbons (TPHs) and polycyclic aromatic hydrocarbons (PAHs), and (4) abundance and composition of benthic macroinfauna. These data were used along with references from previous oil impacts, to estimate the degree of injury and time trajectory for full recovery, which were required to compute injury in units of lost discounted acre-years (DAYs) of marsh ecosystem services.

The marshes were divided into strata reflecting oiling degree and vegetative habitat. Oiling was defined as light, moderate, or heavy. Light oiling referred to less than 10% cover by oil in the initial survey and an oil thickness of < 0.01 cm. Moderate oiling had a coverage of > 10% (average of 60%) and oil thickness > 0.01 cm on marshes downstream from the Swanson Creek source area; these areas were analyzed to determine the extent of the injury. For the light oiling category, all wetland types were combined into a single category. For moderate oiling, the two species, *Spartina alterniflora* and *S.*

cynosuroides, were combined because of very similar responses. Heavily oiled wetlands (those with > 10 % oil cover, > 0.01 cm oil thickness, and location within Swanson Creek) were divided into 6 strata, with shoreline and interior areas for each of the three dominant vegetation types (*Typha spp., S. alterniflora,* and *S. cynosuroides)*. Categories of percent service loss for vegetative services and soil services plus the recovery trajectory were then estimated for each marsh vegetation stratum using best professional judgment. Best professional judgment is inherently inexact. Such judgments employ site-specific observations and historical literature and are the opinion of experts in a given field of study (English et al. 2009). In most cases, these estimations and supporting rationale are peer-reviewed and deemed the best estimate possible. Lightly oiled wetlands (all species combined) were judged to have suffered only a 10% loss in both soil and vegetation services, with complete recovery in 6 months. Moderately oiled *Spartina* marshes were judged to have experienced an initial 50 percent loss in function, with an expected recovery of 1 year for vegetation and 3 years for soils. Table 4.1 summarizes the marsh injury assessment at Chalk Point.

Table 4.1. Summary of marsh injury assessment and recovery trajectory for Chalk Point case (summarized from NOAA et al. 2002)

Injury	Vegetation type	Position in habitat	Estimated service Loss	Predicted 100% recovery time
Lightly oiled			10%	6 months
Moderately oiled	*Spartina alterniflora* & *S. cynosuroides*		50%	vegetation: 1 yr soils: 3 yrs
Heavily oiled	*S. alterniflora*	interior	vegetation: 100%, 50 % @ 1 yr soils: 75%, 25% loss @ 5 yrs	vegetation: 5 yrs soils: 10 yrs
	S. alterniflora	exterior/ edge	vegetation: 100% soils: 75%, 20% loss @ 3 yrs	vegetation: 1 yr soils: 5 yrs
	S. cynosuroides	interior	vegetation: 100%, 50 % @ 1 yr soils: 75%, 50% loss @ 5 yrs	vegetation: 10 yr soils: 20 yrs
	S. cynosuroides	exterior/ edge	vegetation: 100%, 50 % @ 1 yr soils: 75%, 40% loss @ 3 yrs	vegetation: 10 yr soils: 10 yrs
	Typha spp.	interior	vegetation: 100% soils: 50%, 20% @ 5 yrs	vegetation: 1 yr soils: 10 yrs
	Typha spp.	exterior/ edge	vegetation: 100% soils: 75%, 40% loss @ 3 yrs	vegetation: 1 yr soils: 10 yrs

Heavily oiled strata were assigned higher levels of service losses for both vegetation and soils, with soil recovery rate differences between edge and interior locations, based on the reasoning that greater tidal exchange would induce faster dissipation of oil in the edge locations (NOAA et al. 2002). Specifically, heavily oiled *Typha* was assigned a 100% initial service loss to vegetation services in both interior and edge zones, with recovery assumed complete in 1 year. Heavily oiled *Typha* was assigned soil losses of 75% in the edge, recovering to a 40% loss after 3 years and fully recovering after 10 years. Heavily oiled *Typha* in the interior marsh was assigned soil losses of 50% initially, recovering to a 20% loss after 5 years with complete recovery after 10 years. For heavily oiled *Spartina alterniflora*, initial vegetation service loss was assumed to be 100%, with 50% recovery after 1 year and full recovery after 5 years in both interior and edge positions. Soil services were assumed to suffer initial losses of 75% in both interior and edge marshes, with interior recovering to a level of only 25% loss after 5 years and full recovery after 10 years, and edge recovering to a level of 20% loss after 3 years and complete recovery after 5 years. For heavily oiled *Spartina cynosuroides*, initial vegetation service loss was assumed to be 100%, with 50% recovery after 1 year and full recovery after 10 years in both interior and edge positions. Soil services were assumed to suffer initial losses of 75% in both interior and edge marshes, with interior recovering to a level of 50% loss after 5 years and full recovery by 20 years, and edge recovering to a level of 40% loss after 3 years and full recovery after 10 years. Vegetation- and soil-related ecosystem service losses were independently estimated from this injury and recovery scheme in units of lost DAYs. Assuming that vegetation and soil

services of wetlands are equally important, the joint ecosystem service loss was computed by a simple average of the vegetation service loss and the soil service loss in DSAYs.

Lessons from follow-up monitoring

Although I describe the Chalk Point approach as the best available HEA example for assessing injuries to marsh habitat, it is clear that the quantitative data taken during surveys after the spill did not result in an explicitly objective damage assessment; portions of the assessment were subjective. Best professional judgment, informed by field data and past knowledge of marsh injuries and recovery, determined the level of lost marsh ecosystem services assigned. The field observations, especially the repeated observations of plant health and recovery, fed directly into the assignment of the percent initial loss of vegetation services, but this assignment and the recovery trajectory were largely a judgment call. Given that this method represents the best example for assessing injury to one of the most commonly injured and environmentally important habitats, testing its accuracy should be a priority. Michel et al. (2008) provides results of follow-up assessments of how the vegetation and soil recovery had progressed 7 years after oiling of the Chalk Point marshes. This follow-up monitoring took place only in the heavily oiled interior portions of the *Spartina alterniflora* and *Spartina cynosuroides* habitats. Results can be compared against analogous surveys made just after the spill in April 2000, and then in July 2000 and July 2001.

Three metrics were recorded during the 2007 resampling (Michel et al. 2008): (1) persistence and weathering status of PAHs in soils at 0-10 and 10-20 cm depths, (2)

vegetation condition (below-ground biomass, live stem density, and stem height), and (3) surficial soil toxicity in amphipod (*Ampelisca abdita*) bioassays. The results of soil PAH analyses demonstrated that PAH degradation in soils in areas of both species of marsh grass had not decomposed at all in the 7 years since initial sampling after the spill. Furthermore, sediment toxicity testing revealed that half the soil samples were still toxic after 7 years. These results appear to conflict with the recovery trajectories assigned during injury assessment, which presumed that soil services would recover from 25% in 2000 to 75% by 2005 in *S. alterniflora* and 50% in *S. cynosuroides* after 5 years and to 100% after 10 and 20 years, respectively. Vegetation sampling in 2007 revealed that *S. alterniflora* had 37% lower stem densities and 15% lower stem heights and *S. cynosuroides* had 20-35% less belowground biomass, as compared to predictions of complete vegetation recovery in *S. alterniflora* in 5 years and in *S. cynosuroides* in 10 years (NOAA et al. 2002).

Another telling follow-up on long-term recovery dynamics of oiled salt marshes comes from the resampling of Cape Cod marshes over 40 years after the spill from the barge *Florida*. After 40 years, PAHs were detected at 10-20 cm depths in marsh soils and were only moderately degraded. Furthermore, densities of fiddler crabs (*Uca pugnax*) remained lower on oiled marshes than in controls and crabs displayed behavioral differences attributable to possible exposure to toxins. Specifically, burrowing depths of the crabs were only half as deep on the oiled marsh, and crabs on the oiled marsh exhibited sluggish responses to threats relative to control crabs (Culbertson et al. 2007). The soils of the oiled marsh were highly organic and, similar to those of the interior

marsh at Chalk Point, probably largely impervious to oxygen, limiting microbial decomposition processes. The weathering limitations were enhanced by the inability of fiddler crabs to dig normally deep burrows because this process of bioturbation can be valuable in oxygenating deeper sediments and inducing weathering of buried oil.

Evidence from follow-up monitoring at the Chalk Point site and similar evidence collected at the oiled Cape Cod marshes suggest that the recovery curves developed for the Chalk Point assessment underestimated the length of time required for the recovery of oiled marsh. As predicted by Teal and Howarth (1984), heavy oiling of fine-grained salt marsh interiors probably suppresses recovery of at least soil, but also biota for at least four decades and possibly many more. Relatively few long-term follow-up studies exist. However, it is apparent that the information provided from such studies is critical in providing insight and reference where best professional judgment is heavily weighted. Long-term assessments of recovering habitat allow the resource loss and recovery evaluation process to become more objective.

A method to normalize marsh sub-habitat types to estuarine marsh habitat

The Bailey case (Bailey Trustee Council 2003) involved injury of several sub-habitats within a marsh system. The Bailey Waste Superfund Site is a former waste disposal facility in Orange County, Texas. Contaminants [polycyclic aromatic hydrocarbons (PAHs), volatile organic compounds (VOCs), and heavy metals] were found at high concentrations in the sediments and soils of seven different sub-habitat types. The geographic scope of injury of each sub-habitat was determined by using analytical chemistry techniques. The trustees also decided that the level of ecosystem

service loss was 100% in each of these sub-habitats of the marsh system and that these losses are permanent. To facilitate the injury analysis and provide a metric of injury that could readily lead to compensatory restoration, the trustees decided to convert service acre-year (SAYs) losses of each sub-habitat to functionally equivalent SAYs of the brackish marsh sub-habitat because this one was the most extensively injured and it provided potentially the highest level of services under nominal or normal conditions. The relative per-acre values of each of the seven injured sub-habitat types were determined by a "multiple attribute decomposition" process, in which a group of six wetland scientists with knowledge of the local ecosystem (three representing the Responsible Parties and three the natural resource trustees), rated each of the seven habitats from 0 to 10, based upon the perceived value of the joint ecosystem services they provide (e.g., primary productivity, habitat value, nutrient export, etc.). Details of the ecosystem services used for the multiple attribute decomposition were not specified in the report (Bailey Trustee Council 2003). The means of these scores were used to normalize each sub-habitat SAY to an estuarine marsh equivalent (in acres). Once normalized to SAYs of a common habitat type, units are discounted to become DSAYs. Applying this technique, the 3.26 acres of high-marsh habitat that suffered 100% loss, was scaled to have equal ecosystem services equivalent to 1.98 acres of healthy brackish marsh. Table 4.2 illustrates the method and exhibits the score values used to normalize impacts to all sub-habitat types to brackish estuarine marsh losses (Bailey Trustee Council 2003). This injury assessment method resembles the habitat conversion approach in that it provides a metric by which one (sub)-habitat is converted into another in contemplation

of restoration. I present this approach separately because there are some fundamental differences. Here, all habitats that are converted are considered as sub-habitats of a marsh complex not habitats typically recognized as separate. However, I contend that the type or level of ecosystem service differs within sub-habitat type due to differences in parameters such as hydrology and geomorphic setting; such abiotic differences are reflected by the cover type. In addition, the "multiple attribute decomposition" method depends on best professional judgment by a group of experts. This metric is acknowledged as subjective

Table 4.2. Method and rank-score values to normalize habitat impacts to brackish estuarine marsh, Orange County, Texas (Bailey Trustee Council 2003)

Habitat type	Score 1	Score 2	Score 3	Score 4	Score 5	Score 6	Average score	Normalized Average
Brackish tidal marsh	10.0	9.3	10.0	10.0	10.0	9.7	9.833	1.000
High marsh	5.0	6.5	6.0	5.0	7.0	6.3	5.967	0.607
Freshwater marsh	9.0	7.3	7.6	8.0	7.0	7.7	7.767	0.790
Ponds	6.0	4.5	6.3	6.0	5.0	5.2	5.500	0.559
Ditch	5.0	3.5	4.6	3.0	5.0	4.3	4.233	0.431
Upland	2.0	5.3	4.0	4.0	6.0	2.7	4.000	0.407
Road	0.3	2.0	0.6	0.0	1.0	1.0	0.817	0.083

Alternative marsh metrics

Many injury assessments of coastal marshes have been motivated by oil spills and are limited in the scope of quantitative assessment (Peterson 2008a). Even in relatively substantial spills, field assessments in marshes include only (1) documenting the areas of marsh covered by heavy, moderate, and light oiling, (2) measuring stem density and height, perhaps also areal cover, of each dominant vascular plant species within each oiling intensity category, (3) sampling sediments for chemical (petroleum hydrocarbons and PAHs) analyses and depth of contamination, followed by sediment toxicity assays if sediment contamination is high and likely to persist and (4) collecting and counting any dead animals. Other common types of marsh injury involve chronic contaminants by persistent organic pollutants in Superfund sites, where the contaminants may not cause plant injury but necessitate (1) analytic chemistry analyses to compute concentrations of toxicants to compare against known biological effects levels and (2) sediment toxicity testing and toxicological analysis of growth, reproduction, and mortality impacts at higher trophic levels. Marshes provide many ecosystem services (MEA 2005), so reducing metrics to vegetative production of dominant vascular plants and/or sediment injury omits many valued processes, such as biogeochemical cycling and habitat provisioning. An important set of questions arises. Are structural measures of aboveground vegetation of vascular plants the most suitable metric for assessing level of ecosystem services of salt marshes? In addition, should other metrics be added to make this assessment more complete and indicative of either injury level or duration of injury, the two factors needed to estimate service losses?

Peterson et al. (2008a) reviewed several alternative or additional metrics that could provide further quantitative insight into other important ecosystem service levels in marshes. These alternative metrics included: (1) routine stratification of marsh habitat into edge and interior (as done in the Chalk Point 2002 injury assessment (NOAA et al. 2002) with separate sampling in each stratum, (2) microphytobenthos abundance, (3) cotton-strip decomposition bioassays and other biogeochemical indicators, (4) summation of production across consumer trophic levels, and (5) below-ground biomass of vascular plants. Of these, designing marsh sampling to cover edge and interior strata as a routine practice would provide much more resolution of injuries and ensure more confident compensation because the edge typically has higher primary production and food web support than the marsh interior (Anderson and Treshow 1980, Smart 1982, Minello and Zimmerman 1992, Baltz et al. 1993, Minello et al. 1994, Cicchetti and Diaz 2000). The use of microphytobenthos abundance, cotton-strip decomposition bioassays and other biogeochemical indicators, or the summing of consumer production across trophic levels have been deemed by the best professional judgment process as being insufficient as solitary metrics, although their inclusion could aid in the holistic estimation of marsh ecosystem services (Peterson et al. 2008a). In addition, although sampling for belowground biomass is necessarily destructive and damaging, the addition of this information may provide more insight into duration of injury and future productivity. However, more basic research will be needed to develop confidence in the belowground biomass metric and what it implies. Peterson et al. (2008a) concluded that the present metric of aboveground structural plant density is the best single current indicator of

marsh ecosystem services because it correlates with many of the ecosystem services, including primary production, structural habitat provision for fish and wildlife, protection of the shoreline from waves, interception or sediments, nutrients, and pathogens in stormwater flows, aesthetics, carbon storage, and other services. Perhaps no alternative metric relates to so many processes of value in wetlands. In cases where primary production information is important, such as those estimating trophic relationships, a non-destructive estimation of aboveground biomass can be obtained by factoring density with the height of each macrophyte species (Morris and Haskin 1990, Thursby et al. 2002).

Metric-free impact assessment

In small oil spills, where the expense of site-specific injury assessments would be disproportionately high relative to the expected injury, injury to ecosystem services has been estimated on the basis of observed oiling of the marsh with no quantitative injury assessment. Penn and Tomasi (2002) describe the use of oiling categories as a scaling tool to categorize levels of effect from the Lake Barre oil spill assessment. The appropriate relationship between oiling categories and service losses has been examined in detail in several oil spill assessments, including the Chalk Point (NOAA et al. 2002) case, although uncertainty persists. For the Lake Barre case, Penn and Tomasi (2002) describe four recovery trajectories for a salt marsh in Louisiana based on the severity of marsh oiling. The four designations were developed in a collaborative effort between public officials and representatives of Texaco, the company responsible for the spill. The experts relied on previous spill-response experience combined with field observations

during the first year of recovery. Information was collected periodically regarding the persistence of oiling on plants and soils as well as the condition of plants and the presence of invertebrate species in oiled and reference areas. Other resource services such as feeding habitat for birds and spawning habitat for fish were not specifically examined, but were assumed to decline and recover in proportion to the observed variables. The estimated level of injury and recovery trajectories are presented in Table 4.3.

In areas of light oiling ecological services were assumed to decline by 10% initially, and full recovery was assumed after four months. As in all categories presented, the functional form of the predicted recovery path was linear. Heavily oiled areas were divided into three levels of severity. Areas with 40 percent and 75 percent initial service losses were predicted to recover in 2 years based on extent of recovery in the first year following the spill. For areas of 100 percent service loss where all aboveground vegetation was killed, the time required for full recovery was difficult to predict. Because the extent of this severely affected area was limited, the parties agreed to a 20-year recovery horizon that was viewed as a conservative upper-bound estimate. Recent monitoring of the Chalk Point and the lack of recovery of heavily oiled marsh 7 years after the spill (Michel et al. 2008) raises questions about how truly conservative this assumption of a 20-year recovery is.

Clearly, the metric or suite of metrics chosen to best represent the loss of public trust resources is somewhat case specific. Employed metrics need to be appropriate to the type of injury or service loss, be considered in the context of the larger ecosystem

(i.e., marsh habitat within an estuary), and anticipate changes driven by global climate change. It is evident that current methods seek the optimal pragmatic solution to estimate marsh ecosystem services; however, this pragmatism comes at the expense of a just compensation of lost public trust resources. Follow-up monitoring would provide crucial information for validating recovery estimates. In reviewing 37 cases that involved some level of habitat injury, I found several cases in which trustee councils suggested follow-up monitoring to confirm that compensation of lost services of public trust resources were achieved. I found three cases that specified short-term (< 3 years) monitoring to validate recovery trajectories, yet I was unable to obtain these reports. Requiring an investment in monitoring the structure and function of injured, restored and created habitat could advance the goal of appropriately compensating for damages to public trust resources.

Table 4.3. Oiling categories and injury to marsh habitat, Lake Barre, LA (summarized from Penn and Tomasi 2002)

Category of injury	Initial service loss	Time to full recovery
Light oiling	10%	4 months
Heavy oiling, low	40%	2 years
Heavy oiling, medium	75%	2 years
Heavy oiling, high	100%	20 years

Quantifying ecosystem service gain by marsh creation and restoration

Restoring marsh habitat represents an appealing method of compensating for the loss of a wide range of different habitats and the ecosystem services that they provide. Marsh restoration can even be scaled to replace other types of resource losses, such as for guilds like predatory fishes or to individual species populations dependent on marsh habitat (TGLO et al. 2001, Bailey Trustee Council 2003, French McCay et al. 2003, Peterson 2003, Peterson and Lipcius 2003). Coastal marshes have been dramatically depleted in the U. S. (Dahl 1990, 2006) and worldwide (Nicholls et al. 1999, Ladhar 2002, MEA 2005), so their reconstruction makes sense from a perspective of restoring historical baselines and interconnectivity among estuarine habitats. The knowledge of where marshes have existed in the past provides guidance for where marshes may prosper if restored or created. The methods of *S. alterniflora* dominated marsh restoration have been largely resolved, and there is a substantial literature on how to design and install a new salt marsh (e.g., Seneca et al. 1985, Broome et al. 1986, Broome et al. 1998, Warren et al. 2002, Wolters et al. 2008). Coastal marshes are recognized as providers of numerous ecosystem services (MEA 2005, Peterson et al. 2008a), so scaling by use of a proxy to replace one injured service can be assumed to replace several. Because marsh habitat is highly productive and provides numerous ecosystem services per unit area, compensatory restoration can be done efficiently on relatively few acres, thus offering cost savings to responsible parties of NRDA cases.

The most straight-forward scaling of marsh restoration to a service loss involves in-kind replacement of lost acre-years of marsh ecosystem services (SAYs). Such

restorations are quite common, especially as mitigation for unavoidable marsh injuries during land development (Smith et al. 1995, Peterson et al. 2008a). Replacement of lost marsh by new marsh involves few assumptions because the same habitat is involved on both sides of the ledger. The greatest challenge comes in projecting how rapidly the full suite of marsh ecosystem services will return after restoration and what the maximum percent of ecosystem services will be at equilibrium (i.e., A = B in Figure 4.1). The need for such knowledge exists especially when marsh restoration is conducted to restore marsh habitat itself (in-kind restoration) or some other resource (out-of-kind restoration). The most reliable means of ensuring true compensation would be to monitor the injured marsh so as to test assumptions about the trajectory of recovery of the injured marsh after any primary restoration is conducted, and to monitor the same metric(s) in the newly restored marsh as a test of assumptions about development rate of services in both the injured and newly created marsh habitat. This is discussed further in hydrogeomorphic methodology section below. Unfortunately, the responsible parties who must fund the compensatory restoration dislike uncertainty and wish to settle quickly on restoration plans and costs so that incorporating an expensive long-term monitoring of injured and restored marshes to ensure quantitative compensation is not generally feasible. Contingency funds as a percentage of total compensatory restoration costs are collected from settlements of injury liability cases that can provide funding for limited monitoring and limited mid-course corrections of restoration projects (English et al. forthcoming). Conducting more in-depth monitoring in selected systems to allow improvement of estimates of the time course of recovery of ecosystem services in injured and restored

marshes can be done and could improve the projections made in future applications of restoration scaling for tidal marshes.

In a study evaluating created North Carolina marshes between 1 to 28 years of age, Craft et al. (2003) found that most ecological attributes reached equivalency relative to natural reference marshes within 5 to 15 years after construction and that recovery trajectories were predictable. They propose that created marshes follow three general trajectories of recovery and these are associated with hydrological, biological and biogeochemical processes. Most rapid were hydrologic processes such as sedimentation and carbon and nitrogen accumulation that developed immediately, due to having been graded lower than natural marshes. Biological process, such as primary production and heterotrophic activity, reached equivalence over 5 to 15 years. Marsh macrophyte and microphytobenthos biomass achieved levels found in natural marshes in 12-20 years, while invertebrate density reached that of natural marshes in 8 to 13 years. These researchers found stem height to be superior to stem density in predicting aboveground biomass and that heterotrophic process were correlated to surficial (0-10 cm) organic carbon pools (Craft et al. 2003). Biogeochemical processes were slowest to reach natural equivalence. Soil organic carbon and nitrogen pool near the surface (0-30 cm) were slow to develop in created marshes and only few reached equivalence compared to natural marshes even after 28 years. Carbon, nitrogen and phosphorus stored in macro-organic matter was an order of magnitude lower that than in soils and these nutrients accumulated in a predictable manner. Overall, Craft et al. (2003) found that *S. alterniflora* (above- and below- ground biomass) are functional indicators of marsh condition and that soil

organic carbon and nitrogen levels correlated significantly with many marsh ecological attributes in created marshes.

Michel et al. (2008) have monitored both injured and newly constructed (restoring previously converted wetlands from agricultural use) salt marshes after the Chalk Point oil spill on Swanson Creek, Maryland (NOAA et al. 2002). Marsh restoration was completed in October 2005 and Michel et al. (2008) monitored the development of the *S. alterniflora* and *S. cynosuroides* marsh areas in replicate locations 2 m from the creek margin in September 2007. Samples of stem density and height of aboveground vegetation and belowground biomass density over two depths provided the metrics for assessing recovery of marsh ecosystem services, analogous to the injury metrics applied earlier. By comparing the magnitude of each metric in the restored marsh to the levels exhibited at that same time in natural unoiled marsh, Michel et al. (2008) produced quantitative evidence on which to evaluate the initial assumptions about development time of marsh services in the compensatory restoration project. *Spartina alterniflora* stem heights increased in those two years following marsh creation to 95% of natural marsh. Stem densities were 108% of natural marsh values. On the other hand, belowground biomass reached levels of only 39% of natural marsh at the 0-10 cm depth and 7% of natural marsh at 10-20 cm depth. These metric values compare to projections of services development in the restoration scaling for the restored marsh of 50% after 5 years, 75% after 10 years, and 80% after 20 years (NOAA et al. 2002). It seems unlikely that the belowground services of biogeochemical cycling will achieve these projected levels, whereas aboveground services may already have met the anticipated targets well

before anticipated dates. Michel et al. (2008) recognize that the soils at the restoration site were very inorganic and impenetrable. Careful choice or preparation of more organic-rich soils may thus be required for future marsh restorations to achieve assumed rates of return of all ecosystem services, as evidenced by this work in *S. alterniflora* dominant marshes.

One important caution to applying existing metrics to scale the production value of marsh creation relates to the vascular plant species involved in the new marsh. Essentially all of the data available on trophic support of vascular plants growing in salt marshes comes from study of one genus, the *Spartina* grasses. Other vascular plants contribute meaningfully to salt marsh flora. Most prominently, these include *Juncus roemerianus* along the Gulf and south Atlantic coasts, many low-relief succulents like *Salicornia* on the Pacific coast, and invasive species like *Phragmites* spp. and others. As long as the restored marsh consists exclusively of native *Spartina* (perhaps even just *Spartina alterniflora*, which dominates most scientific studies), then the available evidence on primary production and trophic use and transfer efficiencies apply. In cases involving these other vascular plants, use of *S. alterniflora* information produces great uncertainty in actual benefits provided. Use of local species-specific information would make for more confident scaling of the marsh creation.

Marsh restoration has also been used in compensatory scaling for other types of lost services, both habitat injuries like oiling of intertidal or subtidal flats and injuries to resource guilds or species of animals. For both types of compensation, the scaling is more complex and more uncertain than in-kind scaling of lost marsh to restored marsh.

The use of salt marsh restoration to compensate for loss of ecosystem services of subtidal bay bottom in the Lavaca Bay Trustee Council (2000) case record illustrates the scaling that converts one habitat to another. In this instance based on subjective, but informed opinions of experts, who concluded that an acre of fully functional brackish salt marsh provided 5 times the ecosystem services as an acre of bay surface bottom. Consequently, the lost SAYs of bay bottom were replaced by salt marsh in a 5 to 1 ratio (Lavaca Bay Trustee Council 2000).

Newly available habitat conversion ratios based on quantitative productivity ratios computed across all three lowest trophic levels (Peterson et al. forthcoming) represent a more defensible method of scaling future habitat conversions that lead to marsh restoration. These conversion ratios taken from synthesis of production data across three trophic levels suggest that *S. alterniflora* marsh provides about 1.7 times the per acre services as intertidal flat habitat and 2.1 times the services of shallow subtidal habitat (Peterson et al. forthcoming). English et al. (2009) discuss other examples of using created marsh habitat to compensate for the service losses of other types of habitat and taxonomic resources.

Incorporating the hydrogeomorphic approach

The hydrogeomorphic classification (HGM) approach is an accepted functional assessment method that can offer insights to the qualification and quantification of marsh ecosystem services. This approach is routinely employed by the U.S. Army Corps of Engineers in the CWA Section 404 Regulatory Program review process in which wetland functions must be assessed (Cole 2006, USDA and NRCS 2008). In the HGM approach, the functions of a given wetland class are generally dictated by its: (1) geomorphic setting (position within the landscape), (2) water sources (e.g., tidal inundation, precipitation, groundwater and surface flows), and (3) hydrodynamics (e.g., the relative contribution, periodicity and flow direction of each water source) (Brinson 1993, Smith et al. 1995). Once classified, functional indices of wetland types are determined by variables that correspond closely with the level of a wetland attribute (aka. indices or metrics), in a given region. These indices allow the functional assessment of a specified wetland site to be compared to reference standard wetlands within the same class. Hydrogeomorphic-approach uses reference wetlands and reference standards are assumed to be minimally-impacted wetlands that are functioning at high or appropriate levels for their class and are self-sustaining. Specification of a set of reference wetlands within a geographical range, that includes several to many reference sites, thus enables one to capture the range of variation of wetland class within a given region (Christian et al. 2000). There are two sources of variation, natural variability and direct or indirect anthropogenic alterations. Establishing reference standard conditions permits the identification of ultimate restoration goals (Brinson 1993, Brinson and Rheinhardt, 1996, Christian et al. 2000).

The selection of reference sites should account for changes in relative sea-level rise (RSLR), as this process continually alters site hydrology, sedimentation and the biotic community; such abiotic alterations consequently modify ecosystem structure and function (Christian et al. 2000). NRDA cases could benefit from reference standards in locations where such a framework of standards exist. In addition, the HGM approach could be adopted as part of the NRDA process for coastal wetlands.

Within each HGM wetland class, indices representing the specific functions important and unique for that class, in a given region, is established using regional guidebooks, these are readily available on the USACE Environmental Lab website (http://el.erdc.usace.army.mil/wetlands/wlpubs.html) and continue to be developed. Coastal marshes fall within just one large-scale or general class in the HGM classification scheme, tidal fringe wetland:

> Tidal fringe wetlands occur along coasts and estuaries and are under the influence of sea level. They intergrade landward with riverine wetlands where tidal current diminishes and river flow becomes the dominant water source. Additional water sources may be groundwater discharge and precipitation. The interface between the tidal fringe and riverine classes is where bidirectional flows from tides dominate over unidirectional flows controlled by floodplain slope of riverine wetlands. Because tidal fringe wetlands frequently flood and water table elevations are controlled mainly by sea surface elevation, tidal fringe wetlands seldom dry for significant periods. Tidal fringe wetlands lose water by tidal exchange, overland flow to tidal creek channels, and evapotranspiration. Organic matter normally accumulates in higher elevation marsh areas where flooding is less frequent and the wetlands are isolated from shoreline wave erosion by intervening areas of low marsh. *Spartina alterniflora* salt marshes are a common example of tidal fringe wetlands (Smith et al. 1995).

Shafer and Yozzo (2002) further divide coastal fringe wetlands into subclasses based upon three factors: (1) surface hydrology (regular or irregular flooding), (2) salinity

(saline, brackish, or fresh) and vegetation type (marsh or swamp forest). Shafer et al. (2007) address a greater level of functional refinement in their regional guidebook for coastal marshes in the Mississippi and Alabama region of the Gulf of Mexico. These authors describe five functions key to the assessment of this habitat: wave energy attenuation, biogeochemical cycling, nekton utilization potential, habitat provision for tidal marsh-dependent wildlife and maintenance of the characteristic structure and composition of the plant community. Surprisingly, the basic classification parameters (especially hydrodynamics) that dictate marsh ecosystem function have not been incorporated well into the HEA or other NRD assessment approaches to my knowledge.

While specific metrics of ecosystem service (described earlier) have been utilized successfully to assess the degree of habitat injury and recovery, they may not amply represent the functional and service of a public trust resource. In the Chalk Point case described above, the interim loss of injured brackish marsh was compensated for by salt marsh, based upon the dominant vegetation. Here, the degree of vegetative production lost at the injured marsh or gained at the created marsh, was measured relative to a nearby reference marsh of like vegetative cover. However, the different services of brackish and salt marsh ecosystems were not elucidated. Another observation from this case is that the created marsh was established on agricultural lands that were likely previous converted wetlands, and belowground biomass and soil development were slower than professional judgment had anticipated. Nowhere in case study reports did I find mention of the hydrology of the injured or created marsh sites. Hydrological factors may in part be responsible for the slow establishment of the created marsh. Because

hydrological sources and dynamics are key to the function of wetlands and as hydrology greatly influences the type and level of service rendered by this public trust resource, these factors should be considered in the injury assessment and restoration of coastal marsh habitat. The importance of the geomorphic setting and reference was acknowledged and incorporated into assessments at Chalk Point; these are key reasons why Chalk Point was noted as an exemplary case of scaling marsh habitat (English et al. 2009). The use of HGM classification and metrics can aid in replacing like ecosystem services (especially biogeochemical cycling) and may aid in the appropriate selection of restoration sites. In addition, the HGM approach offers a standard methodology by which the function of restored or created marsh habitat can be efficiently measured, once guidelines are established for a given region.

While the HGM approach was established to classify wetlands by similar functions, it was not intended as a valuation procedure. King et al. (2000) expanded the HGM approach by linking function with valuation. Although beyond the scope of this chapter, it is interesting to note that King et al. (2000) describe the Wetland Value Index System that incorporates the value humans place on various wetland ecosystem services.

Climate change considerations

The cumulative effects of global climate change, especially sea-level rise, would be wisely considered in coastal marsh restoration projects. Accelerated rate of sea-level rise is among the most important global climate change phenomena affecting Earth's coastal zones. The IPCC (2007) estimates that eustatic sea level will rise 0.2-0.6 m by 2100. Because coastal marshes occur at the land-sea interface along coastlines with low-sloping topography they are inherently vulnerable to SLR and coastal erosional processes (Hammar-Klose and Thieler 2001). Still, marshes have persisted through millennia of sea level changes by processes such as vertical accretion and horizontal migration across the landscape (Redfield 1965, 1972, Orson et al. 1987, Reed 2002).

Coastal marsh habitat responds not only to rising sea levels (Reed 1993, Morris et al. 2002) and erosion due to increased storminess of a warming global climate (Tiner 1987, Stevenson et al.1988, Meyer et al. 1997, Erwin et al. 2004), but also a host of anthropogenic stressors such as coastal population growth, land use change and habitat destruction, pollution, eutrophication, invasive species, etc (Tiner 1987, Dahl 1990). The interaction of these natural and anthropogenic stressors creates new challenges for marsh sustainability, many of which have been insufficiently anticipated and poorly managed (Cowan et al. 1988, Pethic 2001, Adam 2002, Peterson 2008b). Even as marsh habitat subsists in the presence of accumulating stressors, the level of marsh ecosystem services available to society will likely decrease (Zedler and Kercher 2005, Craft et al. 2009). Because we are limited in our ability to thwart natural stressors, more aggressive protection of marshes would minimize anthropogenic stressors.

Shoreline erosion rates and the landward transgression of marshes in response to sea-level rise can be calculated into restoration and compensatory restoration equations to ensure that the level of public trust resource is maintained for the expected time period. For example, the submersion and erosion components are explicitly parameterized in the scaling computation for a proposed restoration site on East Timbalier, a Louisiana barrier island (LOSCO 1999). The coast of Louisiana is losing coastal wetlands due to RSLR (Boesch et al. 1994), so consideration of marsh loss in scaling restoration benefits is a necessity there because time frames over which the marsh might reasonably persist are long enough that RSLR and erosion will realistically influence the functional area of marsh that does persist. Increasing rates of RSLR and shoreline erosion are now a concern in many other geographic regions, especially south Florida and North Carolina, so loss consideration in marsh restoration scaling is broadly appropriate using locally appropriate rates of relative sea level rise. Furthermore, marsh plants elevate the marsh surface by trapping inorganic sediments aboveground (Leonard and Luther 1995, Morris et al. 2002, Reed 2002) and by belowground production of roots and rhizomes (Cahoon 1998, Turner et al. 2000, Blum and Christian 2004, Nyman et al. 2006). Consequently, modeling of marsh loss over the time frames required for computing benefits of restoration scaling should best address the balance between RSLR and plant-induced elevation of the soil surface. Within the framework of ecosystem state change, high and low marsh habitat transgress up-slope and landwards as sea level rises (Brinson et al. 1995, Christian et al. 2000). Marsh restoration projects that are created seaward of structural barriers like bulkheads are blocked from up-slope transgression and over time

frames in excess of about 20 years, based upon present increasing rates of sea-level rise, will lose marsh area and thus provide annually decreasing ecosystem services (Brinson et al. 1995, Christian et al. 2000, Peterson et al. 2008b). As sea-level rise accelerates, a net loss of coastal marsh habitat is expected (Zedler and Kercher 2005), unless barriers to landward transgression are removed in sufficient time for natural transgression processes to occur (Brinson et al. 1995, Christian et al. 2000, Titus 2000). Therefore, only those restorations in which the upland habitat is in adequate condition and available for up-slope transgression of the marsh, can marsh habitat be assumed to last more than about 20-40 years, depending on local rates of relative sea level rise (Brinson et al. 1995, Christian et al. 2000, Peterson et al. 2008b).

Conclusion

The qualification and quantification of coastal marsh ecosystem services has precedence largely as a result of federal statutes that mandate conservation of the public trust resources that provide these services. Specifically, the Comprehensive Environmental Response Compensation and Liability Act (CERCLA), the Oil Pollution Act (OPA) and the Clean Water Act (CWA) each require responsible parties to compensate for injury through restoration or mitigation that replaced quantitatively the losses. NOAA has been the lead federal agency in overseeing development of this field of compensatory restoration, although other federal agencies, several states, and other nations in the EU are now playing growing roles. The development of the conceptual basis for the field of restoration scaling has coincided with and facilitated the evolution of the fields of natural resource economics and of restoration ecology. Examples of methods to measure such ecosystem services can be derived from cases in which this resource has been injured and compensatory restoration achieved. The selection of metrics that represent the ecological function of coastal marshes is challenging. Determining which metrics best represent lost ecosystem services may vary and are dependent upon the nature of the habitat injury. Macrophyte aboveground density and biomass probably estimate the broadest range of ecosystem services (Peterson et al. 2008a); however, belowground biomass and soil condition also reflect level of ecosystem services (Craft et al. 2003, Peterson et al. 2008a). The level of ecosystem services rendered by coastal ecosystems will be in part determined by the rate of SLR. Evaluating marsh function by considering geomorphic position more accurately assesses level of

ecosystem service rendered (Christian et al. 2000, Peterson et al. 2008a). Developing a reference standard establishes realistic end-points for restoration goals that are specific by region (Christian et al. 2000). Metric selection is also influenced by the societal value of the ecosystem services that are impaired or lost. Perhaps our greatest challenge, in my opinion, remains the appreciation of ecosystem services by coastal managers, decision makers and the general public.

One can anticipate some of the new directions in which restoration scaling may evolve (Peterson and Lipcius 2003). Clearly, research is progressing at the interface of ecology and economics that not only identifies ecosystem services explicitly but also provides quantitative economic valuations for those services (English et al. forthcoming). Research developments can lead to more refined metrics of injury and can serve to improve the economic valuation of injury (Peterson et al. 2008a), useful in those cases where compensation is monetary rather than provided through natural resource restoration projects. As more opportunity to conduct follow-up evaluations of natural recovery and ecological development of newly restored habitats, the assumptions underlying temporal development of ecosystem functions are directly tested (as in Michel et al. 2008). Follow-up testing and ecological research will improve such assumptions in future scaling applications. Within estuarine and coastal systems, connectivity among habitats is great. This implies that the habitat value for any given habitat type is not fixed but varies with landscape setting. Such spatial proximity considerations would affect injury quantification as well as services arising from habitat restorations. As climate change progresses and as the rate of sea-level rise increases, impacts on estuarine habitat

functioning are likely to be great, thus modifying how restoration scaling is computed. Only when marsh ecosystem services are understood and appreciated, will their value be realized.

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Chapter 5. SUMMARY AND SYNTHESIS

The intimate relationship between marsh surface elevation (relative to sea level) and marsh hydrology (chiefly estuarine inundation) determines the persistence of marsh ecosystems and perhaps their ecosystem state. In this body of work I examined the growth response of two dominant marsh macrophytes over a range of inundation periods in an effort to better understand how coastal marshes will respond to the increased flooding and disturbance inherent from sea-level rise. *Spartina alterniflora* Loisel and *Juncus roemerianus* Scheele are the dominant macrophytes in the U.S. southern Atlantic and Gulf coasts, where approximately 90% of U.S. coastal marshes persist. Marsh vegetation is likely key to accretion processes, whereby increased aboveground biomass baffles floodwaters, thus potentially increasing the degree of sedimentation, and increased belowground biomass contributes directly to the elevation of marsh substrate (Cahoon 1998, Morris et al. 2002). Significant trends of decreasing macrophyte production with increasing inundation were observed across most response variables measured. The aboveground production patterns of *S. alterniflora* and *J. roemerianus* responded similarly to inundation period, though I found that *S. alterniflora* tolerated a greater degree of inundation than did *J. roemerianus*. *Juncus roemerianus* demonstrated a greater stress response at the astronomically-dominated inundation site (PKS) compared to the meteorologically-dominated inundation site (LOLA) at comparable inundation periods, as the less energetic site (LOLA) showed significantly greater end-of-season live aboveground biomass and less senescence at the end of the 2006 growing season. The experimental design employed for this research allowed me to determine the range where

inundation thresholds most likely occur. I observed essentially no seasonal increase in *S. alterniflora* biomass at elevations inundated ≥ 67 % (PKS only) and no seasonal increase in *J. roemerianus* biomass at elevations inundated ≥ 42 % and ≥ 53 % at PKS and LOLA, respectively. In addition, *S. alterniflora* culms and *J. roemerianus* leaves were largely dead at elevations inundated ≥ 92 % and ≥ 42 to 53 %, respectively.

The net above- and below- ground growth responses of *S. alterniflora* and *J. roemerianus* were similar when these species were cultivated in mesocosms individually and jointly over a range on inundation periods. My results showed no significant interaction between *S. alterniflora* and *J. roemerianus* with inundation period. In multi-level co-planted marsh mesocosms, *S. alterniflora* aboveground material contributed proportionally more in net seasonal production over *J. roemerianus*. It was unclear whether the greater proportional production of *S. alterniflora* was due to its greater inundation tolerance or the natural senescence of *J. roemerianus*. I was unable to define an interaction between these two dominant marsh macrophytes with duration of inundation.

My results showed that the macrophyte growth response to inundation in multi-level marsh mesocosms reflected that of marsh platforms. Edaphic conditions likely differed between the mesocosms and platform for a given inundation period, as high elevation mesocosm rows experienced greater drainage and low elevation rows experienced less drainage, compared to the marsh platform. However, this difference allowed me to consider the vertical and lateral effect of hydraulic head (e.g., that inherent with increasing sea levels) present in marsh interior zones which may experience

hydraulic isolation. Site differences in tidal range (tidal pumping) and its affect on edaphic conditions may also explain peak biomass occurring at different elevations relative to MSL. We propose that determining inundation period, rather than elevation, may allow more accurate predictions of macrophyte production.

The use of multi-level marsh mesocosms has improved our understanding of macrophyte response to inundation. Within marsh habitat, macrophyte populations experience two divergent gradients of aerobic-to-anaerobic edaphic conditions with estuarine inundation being a subsidy-stress phenomenon. At some midpoint frequencies, estuarine inundation provides an energy subsidy to marsh interior zones, releasing macrophytes from hydraulic isolation, altering edaphic conditions (decreasing soil toxins and salinity) and aerating soils with tidal pumping and providing a sediment source. At an optimum degree of inundation, macrophyte production is greatest. Greater inundation frequency becomes a stressor to marsh macrophytes, saturating marsh soils and altering edaphic conditions (increasing anoxia) to a point at which inundation frequency causes individual plants to die. In addition, I propose that inundation can elicit a stress response in marsh macrophytes (i.e., *S. alterniflora*) triggering macrophytes to grow taller. An increase in height benefits frequently submerged macrophytes by creating more leaf area that remains aerial, allowing some degree of photosynthesis to continue during submergence; subsequently, oxygen is transported to aerenchyma tissue in the roots and thus provides a mechanism to aerate marsh soils (Howes et al. 1986). More work is needed to examine this mechanism as it relates to macrophyte height, although others

(Laan and Blom 1990, Blom and Voesenek, Insausti et al. 2001) have observed a shoot elongation response to submergence in other species.

My results contribute to a growing body of evidence that shows that belowground biomass is positively correlated with elevation (Blum 1993, Widdows et al. 2008). Such observations suggest that the greatest macro organic matter contributions are made at higher elevations and that these contributions account for a greater proportion of vertical accretion in the high as compared to the low marsh zone. This bioaccretion process may be especially critical for marshes to keep pace with sea level rise in estuaries where little inorganic sediment is available.

Because both above- and below- ground biomass decreased with increasing inundation, I predict that similar marsh ecosystems in North Carolina will be unable to accrete sufficiently to maintain elevation relative to accelerating rising sea levels. Marsh ecosystems accrete vertically via the processes of sedimentation and bioaccretion. As marsh macrophytes respond to increased inundation, consequential decreases in aboveground biomass will likely decrease the ability of marsh macrophytes to entrap estuarine sediments (as per Morris et al. 2002). Likewise, decreases in belowground biomass will decrease bioaccumulation contributions to accretion. A reduction in above- and below- ground biomass results in a positive feedback of a lower elevation relative to sea level, greater inundation and a further reduction in macrophyte biomass. Hence, it appears that if the extent of North Carolina marshes are to persist, we must allow for their landward transgression where geomorphologically feasible.

Juncus roemerianus showed poor resilience to both pulsed and repeated press disturbance. In marsh mesocosms, *J. roemerianus* illustrated a stress response within the more energetic, astronomically-dominated inundation regime, as noted above. The response variables that differed significantly between the two sites occurred at elevations most likely to receive frequent wind-driven wave energy. The difference in wave energy was considered to be significant between sites because the fetch length experienced by the mesocosms at PKS was greater by a factor of thirty. In experimental plots on the marsh platform, the percent cover of *J. roemerianus* was significantly reduced after a pulse disturbance (cutting), which simulated a fire or devegetation event; the reduction in cover was significant within both inundation regimes. The percent cover of *S. alterniflora* significantly increased in disturbed *J. roemerianus* plots established along the *S. alterniflora* - *J. roemerianus* interface. The sensitivity of *J. roemerianus* to repeated press (wave action) and pulse (cutting) disturbance could explain observations of *J. roemerianus*-dominated marshes being fringed by *S. alterniflora* in astronomically-dominated estuaries. This also explains contrasting observations of *J. roemerianus* occurring along the estuarine edge in meteorologically-dominated marshes, where overall energy regimes are relatively lower. *Spartina alterniflora* will likely replace *J. roemerianus* in shore zones where these macrophytes occur and where energy regimes increase in response to global climate change.

Ecosystem disturbances can be viewed as events or processes that reset the successional 'clock' (Sousa 1984, Turner et al. 2003). The findings in chapters 2 and 3 support the conceptual model of ecosystem state change proposed by Brinson et al.

(1995) and Christian et al. (2000) in which the effects of a press disturbance (e.g., sea-level rise) may be less evident than the effects of pulsed disturbances (e.g., wrack deposition, fire, wave action), which may push an ecosystem state beyond the threshold of returning to the same state. However, it is the press disturbance that moves the threshold closer to the tipping point and the pulsed disturbance that ultimately results in a change of ecosystem state (Brinson et al. 1995, Christian et al. 2000). Sea-level rise is a press disturbance (e.g., increased inundation) that continually shifts the tolerance range of organisms in a landward direction. Under a scenario of accelerating SLR, organisms may be displaced further landward with each pulsed disturbance (e.g., storm, fire, wrack deposition). Perhaps such cumulative disturbances serve as a mechanism that drives the transgression process on a landscape scale. Understanding the role of disturbance type, frequency and severity, as well as that of cumulative effects, is an area of research requiring more attention given the anticipated impacts of global climate change.

The quantification of coastal marsh ecosystem services has been achieved broadly by methodologies utilized by the Natural Resource Damage Assessment process. This method currently employs only a few metrics to assess the ecosystem services rendered by an entire ecosystem type. Peterson et al. (2008) have evaluated alternatives to the current method for measuring marsh ecosystem services and state that the density of aboveground vegetation is the most developed, single quantitative metric to date. Macrophyte aboveground density corresponds to many of the ecosystem services provided by marshes, including primary production, structural habitat provision for fish and wildlife, protection of the shoreline from waves, interception of sediments, nutrients,

and pathogens in stormwater flows, aesthetics, carbon storage, and other services. It is apparent that more research is needed to develop further metrics, or a suite of metrics, that comprehensively reflect marsh ecosystem functions and the services rendered to human societies. Synthesis of current methods used to assess ecosystem services found that U.S. statutes provide for the compensation of loss of public trust resources, yet current metrics for ecosystem services serve as incomplete proxies of ecosystem function and condition. We have much to learn regarding the manner in which ecosystem functions are translated into the ecosystem services that are exploited by society. Additional research and education are needed if we are to understand the relevance of ecosystem services and their benefit to society.

The type and level of ecosystem service provided by a given habitat remains in constant flux, as ecosystem components respond to a dynamic environment and to one another. To a degree, such dynamics (e.g., inundation regime) serve to homogenize marsh characteristics across geographic scales, limiting the range of organisms present and defining basic community structure. Yet, dynamics can also be somewhat site specific and hence, challenge our ability to discern appropriate reference and a representative assessment of ecosystem function. For example, aboveground density has been found to serve as the best single proxy of marsh ecosystem services (Peterson et al. 2008), as described above. Marsh macrophyte density and biomass may be similar between two marshes despite the fact that they occur within different inundation regimes, as was the case between PKS and LOLA. Faunal use, trophic relationships and biogeochemical cycling would likely differ by inundation regime as well (Voss 2006,

Craft et al. 2009). One might expect the impact of an oil spill to be greater at the LOLA marsh, compared to PKS marsh, due to the lack of relative flushing that occurs at the LOLA site. This study joins others to suggest that several aspects of marsh habitat function differently between sites, even when cursory assessments (e.g., species presence and biomass density) may indicate their similarity. Assumptions that link ecological function of unaltered and altered marsh habitat based on only few parameters should be derived cautiously and need to be considered within the context of the larger ecosystem.

Coastal marsh ecosystems are well adapted to the dynamics inherent to the coastal zones in which they occur. The fact that coastal marsh ecosystems have persisted for millennia and that they are well adapted to an array of disturbances bodes well for their fate, so long as human interventions do not hinder in the evolution of these ecosystems. My research suggests that at least some coastal marsh systems will be challenged in their ability to accrete vertically at a rate sufficient to maintain elevation relative to accelerated rising sea levels; hence, the landward transgression of these ecosystems is likely key to their persistence. Also interesting is conceiving how coastal ecosystems will manage the increase in energy resulting from the warming of Earth. The heating and cooling of our planet has occurred repeatedly on Earth's geological time-scale; however, the accelerating rate of change that our planet is now experiencing has not occurred during the existence of humankind (Hoegh-Guldberg et al. 2007, IPCC 2007). With approximately 10% of global human populations living less than 10 m above sea level (McGranahan et al. 2007), interactions of biotic (including anthropogenic) and abiotic

processes at this marine-terrestrial interface will surely prove to be extraordinary and challenge our goal of sustainability within the coastal zone.

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Appendix A. Demographics of *Spartina alterniflora* cultivated in pots in multi-level marsh planter at Pine Knoll Shores, NC in September 2006 (each pot = 0.01818 m^2) [ns = no sample]

Pot	Row	Total culm length green (cm/pot)	Total culm length brown (cm/pot)	Total culm length (cm/pot)	Total No. of culms (pot)	Live culm wt. (gdw/pot)	Dead culm wt.(gdw/pot)	Total culm weight (gdw/pot)	Total macro-organic matter (afdg/pot)
1	1	ns	ns	ns	ns	ns	ns	ns	2.69
2	1	244.1	75.2	319.3	13	3.53	1.58	5.11	33.68
3	1	220.7	48	268.7	13	3.08	1.21	4.29	50.95
4	1	167.2	41.6	208.8	10	2.37	1.07	3.44	61.93
5	1	ns	ns	ns	ns	ns	ns	ns	65.73
6	1	168.6	20.4	189	7	0.6	0.26	0.86	53.94
7	2	ns	ns	ns	ns	ns	ns	ns	71.84
8	2	202.6	36.8	239.4	7	4.33	3.64	7.97	66.18
9	2	362.7	62	424.7	23	6.94	2.78	9.72	53.95
10	2	ns	ns	ns	ns	ns	ns	ns	49.87
11	2	ns	ns	ns	ns	ns	ns	ns	68.73
12	2	ns	ns	ns	ns	ns	ns	ns	40.23
13	3	ns	ns	ns	ns	ns	ns	ns	49.72
14	3	ns	ns	ns	ns	ns	ns	ns	ns
15	3	ns	ns	ns	ns	ns	ns	ns	78.77
16	3	ns	ns	ns	ns	ns	ns	ns	50.89
17	3	ns	ns	ns	ns	ns	ns	ns	98.27
18	3	ns	ns	ns	ns	ns	ns	ns	60.52
19	4	ns	ns	ns	ns	ns	ns	ns	113.70
20	4	ns	ns	ns	ns	ns	ns	ns	65.83
21	4	ns	ns	ns	ns	ns	ns	ns	70.70
22	4	ns	ns	ns	ns	ns	ns	ns	103.81
23	4	520.7	48.9	598.9	18	12.83	2.02	14.85	44.05
24	4	ns	ns	ns	ns	ns	ns	ns	306.14
25	5	ns	ns	ns	ns	ns	ns	ns	85.60
26	5	322.2	52.6	374.8	20	6.04	1.72	7.76	120.78
27	5	ns	ns	ns	ns	ns	ns	ns	57.61
28	5	ns	ns	ns	ns	ns	ns	ns	110.41
29	5	ns	ns	ns	ns	ns	ns	ns	133.58
30	5	466.5	378.2	844.7	30	13.48	10.35	23.83	127.89
31	6	139.5	282.7	422.2	21	2.76	5.59	8.35	99.94
32	6	ns	ns	ns	ns	ns	ns	ns	123.06
33	6	ns	ns	ns	ns	ns	ns	ns	80.25
34	6	508.5	104.8	581.9	16	16.65	2.15	18.8	160.59
35	6	442.4	163.3	605.7	19	11.07	3.47	14.54	61.07
36	6	ns	ns	ns	ns	ns	ns	ns	113.24

Appendix B. Demographics of J*uncus roemerianus* cultivated in pots cultivated in multi-level planters at Pine Knoll Shores, NC in September 2006 (each pot = 0.01818 m^2)

Pot	Row	Total leaf length green (cm/pot)	Total leaf length brown (cm/pot)	Total leaf length (cm/pot)	Total No. of Leaves (pot)	Live leaf wt. (gdw/pot)	Dead leaf wt.(gdw/pot)	Total leaf weight (gdw/pot)	Total macro-organic matter (afdg/pot)
1	1	0	399	399	27.0	0.00	9.29	9.29	57.82
2	1	0	288.7	288.7	15.0	0.00	5.73	5.73	75.39
3	1	0	341.9	341.9	16.0	0.00	9.86	9.86	144.30
4	1	0	124.2	124.2	7.0	0.00	2.77	2.77	38.55
5	1	0	291.1	291.1	20.0	0.00	8.31	8.31	118.68
6	1	0	255.3	255.3	15.0	0.00	5.19	5.19	97.03
7	2	0	250.9	250.9	14.0	0.00	6.96	6.96	48.94
8	2	0	89.7	89.7	7.0	0.00	2.73	2.73	32.07
9	2	0	201.3	201.3	13.0	0.00	6.37	6.37	77.66
10	2	65.3	567.6	632.9	33.0	0.63	10.56	11.19	168.41
11	2	0	205	205	11.0	0.00	6.21	6.21	53.25
12	2	0	708.5	708.5	37.0	0.00	19.88	19.88	91.06
13	3	0	128.8	128.8	9.0	0.00	2.60	2.60	60.85
14	3	84.1	479	563.1	18.0	1.37	10.15	11.52	4.79
15	3	72.2	277	349.2	16.0	0.84	5.09	5.93	112.38
16	3	272.3	860.9	1133.2	32.0	3.56	15.21	18.77	120.28
17	3	281.6	1329.3	1610.9	48.0	4.86	23.72	28.58	64.73
18	3	201.5	1018.8	1220.3	32.0	3.50	21.71	25.21	67.70
19	4	392.3	1241.06	1633.36	43.0	6.30	27.35	33.65	79.98
20	4	224.4	1027.7	1252.1	55.0	2.91	20.41	23.32	93.85
21	4	82.9	743.6	826.5	31.0	8.63	10.69	19.32	74.44
22	4	74.9	130	204.9	7.0	1.01	2.83	3.84	42.79
23	4	48.2	225.7	273.9	14.0	0.59	3.84	4.43	78.58
24	4	229.1	513	742.1	33.0	2.87	6.58	9.45	98.86
25	5	579.5	1209.6	1789.1	54.0	7.82	17.12	24.94	161.40
26	5	965.8	1370.3	2336.1	45.0	14.71	20.38	35.09	77.31
27	5	269.5	386.8	656.3	29.0	1.86	8.71	10.57	96.68
28	5	352	753.5	1105.5	24.0	7.49	8.21	15.70	94.14
29	5	727.3	1091.1	1818.4	41.0	9.81	8.80	18.61	58.66
30	5	153.3	373.2	526.5	18.0	2.64	7.02	9.66	107.75
31	6	245.3	452.5	697.8	19.0	2.85	7.07	9.92	165.07
32	6	290.4	485.3	775.7	29.0	3.76	12.64	16.40	157.97
33	6	446.61	517.89	964.5	26.0	6.23	5.70	11.93	87.77
34	6	803.8	1890.36	2694.16	73.0	10.53	27.56	38.09	156.70
35	6	750.4	1155.5	1905.9	46.0	11.59	15.87	27.46	169.21
36	6	88.1	314.5	402.6	22.0	1.08	5.27	6.35	109.08

Appendix C. Demographics of J*uncus roemerianus* cultivated in pots in multi-level marsh planter at Lola, NC in September 2006 (each pot = 0.01818 m^2)

Pot	Row	Total leaf length green (cm/pot)	Total leaf length brown (cm/pot)	Total leaf length (cm/pot)	Total No. of Leaves (pot)	Live leaf wt. (gdw/pot)	Dead leaf wt.(gdw/pot)	Total leaf weight (gdw/pot)	Total macro-organic matter (afdg/pot)
1	1	0	273.4	273.4	27	0.00	7.98	7.98	66.07
2	1	0	410.9	410.9	31	0.00	10.16	10.16	51.20
3	1	0	340.1	340.1	31	0.00	13.43	13.43	62.83
4	1	0	133.6	133.6	16	0.00	5.64	5.64	69.88
5	1	0	303.1	303.1	25	0.00	7.51	7.51	38.28
6	1	0	88.5	88.5	8	0.00	2.22	2.22	73.12
7	2	0	169.5	169.5	19	0.00	4.67	4.67	36.74
8	2	24.4	198.1	222.5	10	0.00	2.28	2.28	73.22
9	2	146.9	597	743.9	29	1.20	3.76	4.96	87.28
10	2	0	394.8	394.8	21	0.00	9.62	9.62	66.49
11	2	132.7	370.1	502.8	18	0.75	4.62	5.37	63.98
12	2	0	199.8	199.8	18	0.00	3.26	3.26	90.24
13	3	324.3	783	1107.3	28	3.12	10.39	13.51	86.37
14	3	796	1929	2725	67	6.99	19.53	26.52	67.14
15	3	251.4	1148.2	1399.6	37	1.94	23.28	25.22	89.57
16	3	319.4	662.7	982.1	35	2.80	5.15	7.95	114.99
17	3	1074.7	2410.7	3485.4	68	14.34	25.68	40.02	91.22
18	3	471.6	877	1348.6	50	0.00	4.86	4.86	91.14
19	4	806.3	1062	1868.3	37	8.58	15.07	23.65	108.86
20	4	1096.3	1365.4	2461.7	55	12.63	12.94	25.57	132.14
21	4	993.4	1605.4	2598.8	52	12.62	18.21	30.83	132.32
22	4	402.4	480.6	883	27	3.46	5.44	8.90	84.61
23	4	1053.5	1571.5	2625	45	16.56	16.79	33.35	91.05
24	4	263.4	758.7	1022.1	50	2.94	6.89	9.83	84.50
25	5	749.3	1774.2	2523.5	71	2.19	19.64	21.83	125.69
26	5	979.7	1398	2377.7	49	14.58	13.26	27.84	89.99
27	5	1269.2	1477.7	2746.9	66	10.98	16.29	27.27	90.69
28	5	314.5	505.6	820.1	29	3.28	5.45	8.73	68.22
29	5	1970.1	2206.3	4176.4	86	28.79	12.41	41.20	177.27
30	5	122.6	529.5	652.1	26	1.64	5.74	7.38	52.36
31	6	1729.3	2152.1	3881.4	30	4.11	6.14	10.25	108.93
32	6	1729.3	2152.1	3881.4	88	21.06	12.16	33.22	125.94
33	6	1068.8	1942.9	3011.7	54	13.15	11.90	25.05	101.77
34	6	528.9	846.01	1374.91	42	3.73	8.61	12.34	95.40
35	6	500.1	928.6	1428.7	38	5.29	10.81	16.10	84.42
36	6	134.5	383	517.5	24	1.42	4.64	6.06	118.35

Appendix D. Demographics of *Spartina alterniflora* in elevational-equivalent plots at Pine Knoll Shores, NC in September 2006 (each sample = 0.01818 m^2) [note: hundredths place number correlates to elevational-equivalent planter row]

Sample	Total culm length green (cm/sample)	Total culm length brown (cm/sample)	Total culm length (cm/sample)	Total No. of culms (sample)	Live culm wt. (gdw/sample)	Dead culm wt.(gdw/sample)	Total culm weight (gdw/sample)
102	305.8	29.1	334.9	9	7.77	0.44	8.21
104	482	139.8	621.8	13	14.998	2.38	17.378
105	506.2	380.6	886.8	24	9.33	8.35	17.68
106	453.3	233.3	686.6	17	8.09	5.77	13.86
107	545.6	109.7	655.3	14	10	1.8	11.8
201	285.7	75.5	361.2	12	7.09	0.48	7.57
202	82.6	0	82.6	3	2.5	0	2.5
203	326.2	86.2	412.4	16	8.57	1.41	9.98
204	202.1	43.2	245.3	8	6.19	0.28	6.47
205	271.9	89.1	361	12	7.82	2.34	10.16
301	219.8	88.1	307.9	8	10.23	0.79	11.02
307	185.4	156.5	341.9	9	7.76	3.68	11.44
401	350	59.4	409.4	10	8.25	1.81	10.06
404	230.6	404.7	635.3	17	4.26	6.12	10.38
405	195	213.6	408.6	7	8.22	5.22	13.44
406	40.6	10.6	51.2	3	1.64	0.15	1.79
407	133.1	19.4	152.5	4	3.66	0.32	3.98
408	115.7	57.9	173.6	4	5.75	2.16	7.91

Appendix E. Demographics of *Juncus roemerianus* in elevational-equivalent plots at Pine Knoll Shores, NC in September 2006 (each sample = 0.01818 m^2) [note: hundredths place number correlates to elevational-equivalent planter row]

Sample	Total leaf length green (cm/sample)	Total leaf length brown (cm/sample)	Total leaf length (cm/sample)	Total No. of Leaves (sample)	Live leaf wt. (gdw/sample)	Dead leaf wt.(gdw/sample)	Total leaf weight (gdw/sample)
301	1018.2	640.5	1658.7	23	16.16	4.42	20.58
302	708.8	464.9	1173.7	20	6.53	8.9	15.43
303	550.3	381.3	931.6	18	10.47	5.76	16.23
304	359.2	314.9	674.1	13	3.9	1.43	5.33
305	919.7	621.9	1541.6	26	11.57	5.03	16.6
306	992	1465.1	2457.1	45	14.37	19.14	33.51
401	ns	ns	ns	ns	ns	ns	ns
402	ns	ns	ns	ns	ns	ns	ns
403	474.9	161	635.9	10	5.96	1.43	7.39
404	676.8	231.3	908.1	13	8.68	1.53	10.21
405	ns	ns	ns	ns	ns	ns	ns
406	ns	ns	ns	ns	ns	ns	ns

Appendix F. Demographics of *Juncus roemerianus* in elevational-equivalent plots at Lola, NC in September 2006 (each sample = 0.01818 m^2) [Samples obtained from three separate plots, all elevationally-equivalent to row 4 of respective planter]

Sample	Total leaf length green (cm/sample)	Total leaf length brown (cm/sample)	Total leaf length (cm/sample)	Total No. of Leaves (sample)	Live leaf wt. (gdw/sample)	Dead leaf wt.(gdw/sample)	Total leaf weight (gdw/sample)
401	512.4	956	1468.4	22	6.37	10.58	16.95
402	692.2	692.9	1385.1	21	7.69	8.64	16.33
403	934.7	537.8	1472.5	24	11.95	6.09	18.04
404	349.2	944.8	1294	30	3.07	12.67	15.74
405	543.2	952.5	1495.7	31	5.12	11.94	17.06
406	1180.3	700	1880.3	34	17.92	19.14	27.06
451	411.2	353.3	764.5	16	7.41	3.82	11.23
452	1317.1	626.2	1943.3	30	5.16	6.92	12.08
453	964.3	1159.9	2124.2	30	17.97	7.83	25.8
454	779.2	698.7	1477.9	24	9.1	11.02	20.12
455	871.3	1134.6	2005.9	33	12.94	7.51	20.45
456	699.1	627.2	1326.3	23	7.55	8.45	16
457	1438	922	2360	41	17.51	6.45	23.96
4001	345.8	433.4	779.2	10	2.96	3.33	6.29
4002	823.2	1161.7	1984.9	25	8.63	10.83	19.46
4003	634.7	607.4	1242.1	20	5.4	5.81	11.21
4004	563.7	1336.6	1900.3	30	6.48	11.04	17.52
4005	381.3	215	596.3	10	2.21	1.07	3.28
4006	500.2	650	1150.2	14	7.16	3.74	10.9

Appendix G. Demographics of *Spartina alterniflora* and *Juncus roemerianus* co-planted in pots in multi-level marsh planter at Pine Knoll Shores, NC in September 2007 (each pot = 0.01818 m^2) [ns = no sample]

		Juncus roemerianus							*Spartina alterniflora*								both spp.
Pot	Row	Total leaf length green (cm/pot)	Total leaf length brown (cm/pot)	Total leaf length (cm/pot)	Total No. of leaves (pot)	Live leaf wt. (gdw/pot)	Dead leaf wt.(gdw/pot)	Total leaf weight (gdw/pot)	Total culm length green (cm/pot)	Total culm length brown (cm/pot)	Total culm length (cm/pot)	Total No. of leaves (pot)	Total No. of culms (pot)	Live culm wt. (gdw/pot)	Dead culm wt.(gdw/pot)	Total culm weight (gdw/pot)	Total macro-organic matter (afdg/pot)
1	1	0.0	164.5	164.5	16	0.00	5.00	5.00	0.0	0.0	0.0	0	0	0.00	0.00	0.00	62.57
2	1	0.0	20.0	20.0	5	0.00	0.52	0.52	0.0	0.0	0.0	0	0	0.00	0.00	0.00	ns
3	1	0.0	111.0	111.0	11	0.00	3.25	3.25	0.0	0.0	0.0	0	0	0.00	0.00	0.00	44.96
4	1	0.0	38.0	38.0	4	0.00	1.49	1.49	0.0	0.0	0.0	0	0	0.00	0.00	0.00	56.75
5	1	0.0	184.0	184.0	15	0.00	6.54	6.54	0.0	0.0	0.0	0	0	0.00	0.00	0.00	39.79
6	1	0.0	40.5	40.5	3	0.00	1.15	1.15	0.0	0.0	0.0	0	0	0.00	0.00	0.00	38.78
7	2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
8	2	0.0	28.5	28.5	2	0.00	0.83	0.83	0.0	0.0	0.0	0	0	0.00	0.00	0.00	38.72
9	2	0.0	138.0	138.0	14	0.00	4.22	4.22	0.0	0.0	0.0	0	0	0.00	0.00	0.00	54.78
10	2	0.0	8.5	8.5	3	0.00	0.12	0.12	0.0	0.0	0.0	0	0	0.00	0.00	0.00	33.92
11	2	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	90.40
12	2	0.0	111.5	111.5	18	0.00	5.22	5.22	0.0	0.0	0.0	0	0	0.00	0.00	0.00	28.61
13	3	0.0	78.5	78.5	9	0.00	4.85	4.85	0.0	0.0	0.0	0	0	0.00	0.00	0.00	46.87
14	3	0.0	46.5	46.5	3	0.00	1.36	1.36	0.0	0.0	0.0	0	0	0.00	0.00	0.00	58.54
15	3	0.0	75.5	75.5	7	0.00	4.47	4.47	0.0	0.0	0.0	0	0	0.00	0.00	0.00	24.33
16	3	0.0	30.0	30.0	3	0.00	0.79	0.79	106.0	0.0	106.0	18	4	1.52	0.00	1.52	25.27
17	3	0.0	16.0	16.0	1	0.00	0.93	0.93	0.0	0.0	0.0	0	0	0.00	0.00	0.00	44.04
18	3	0.0	50.5	50.5	3	0.00	1.46	1.46	0.0	0.0	0.0	0	0	0.00	0.00	0.00	23.08

Appendix G (cont'd). Demographics of *Spartina alterniflora* and *Juncus roemerianus* co-planted in pots in multi-level marsh planter at Pine Knoll Shores, NC in September 2007 (each pot = 0.01818 m^2) [ns = no sample]

Juncus roemerianus									*Spartina alterniflora*								both spp.
Pot	Row	Total leaf length green (cm/pot)	Total leaf length brown (cm/pot)	Total leaf length (cm/pot)	Total No. of leaves (pot)	Live leaf wt. (gdw/pot)	Dead leaf wt.(gdw/pot)	Total leaf weight (gdw/pot)	Total culm length green (cm/pot)	Total culm length brown (cm/pot)	Total culm length (cm/pot)	Total No. of leaves (pot)	Total No. of culms (pot)	Live culm wt. (gdw/pot)	Dead culm wt.(gdw/pot)	Total culm weight (gdw/pot)	Total macro-organic matter (afdg/pot)
19	4	0.0	150.5	150.5	14	0.00	3.90	3.90	0.0	0.0	0.0	0	0	0.00	0.00	0.00	31.65
20	4	0.0	193.0	193.0	12	0.00	17.03	17.03	228.0	22.0	250.0	62	11	5.88	0.00	5.88	47.00
21	4	0.0	46.0	46.0	7	0.00	1.11	1.11	113.5	11.5	125.0	31	8	2.09	0.00	2.09	28.58
22	4	0.0	44.5	44.5	3	0.00	2.51	2.51	148.0	6.0	154.0	26	5	3.77	0.00	3.77	22.84
23	4	0	298.5	298.5	11	0.00	12.26	12.26	133.5	9.0	142.5	28	6	3.00	0.00	3.00	51.61
24	4	0.0	33.0	33.0	1	0.00	1.72	1.72	76.0	51.0	127.0	23	5	1.64	0.69	2.33	16.64
25	5	0.0	82.5	82.5	4	0.00	3.79	3.79	93.0	9.5	102.5	35	7	2.14	0.00	2.14	12.60
26	5	0.0	137.5	137.5	8	0.00	4.59	4.59	145.0	0.0	145.0	46	8	4.30	0.00	4.30	52.01
27	5	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
28	5	0.0	243.5	243.5	15	0.00	5.24	5.24	281.5	48.0	329.5	86	17	6.26	0.37	6.63	62.10
29	5	0.0	360.0	360.0	21	0.00	9.81	9.81	114.5	0.0	114.5	37	7	2.41	0.00	2.41	21.64
30	5	0.0	306.5	306.5	15	0.00	5.37	5.37	36.0	0.0	36.0	13	2	0.88	0.00	0.88	33.81
31	6	107.0	446.0	553.0	14	1.18	4.30	5.48	141.5	0.0	141.5	36	6	3.77	0.42	4.19	67.30
32	6	13.5	488.0	501.5	17	0.31	12.81	13.12	243.0	45.0	288.0	76	14	8.77	1.19	9.96	88.95
33	6	0.0	336.5	336.5	15	0.00	6.29	6.29	0.0	0.0	0.0	0	0	0.00	0.00	0.00	62.74
34	6	5.5	101.0	106.5	4	0.00	2.06	2.06	220.5	20.0	240.5	78	13	5.89	0.00	5.89	61.41
35	6	0.0	338.5	338.5	9	0.00	7.56	7.56	62.5	0.0	62.5	25	4	0.91	0.00	0.91	30.44
36	6	0.0	426.0	426.0	14	0.00	6.44	6.44	91.5	10.5	102.0	36	7	3.03	0.38	3.41	73.91

Appendix H. Demographics of *Spartina alterniflora* and *Juncus roemerianus* co-planted in pots in multi-level marsh planter at Lola, NC in September 2007 (each pot = 0.01818 m^2) [ns = no sample]

Juncus roemerianus									*Spartina alterniflora*							both spp.
Pot	Row	Total leaf length green (cm/pot)	Total leaf length brown (cm/pot)	Total leaf length (cm/pot)	Total No. of leaves (pot)	Live leaf wt. (gdw/pot)	Dead leaf wt. (gdw/pot)	Total leaf weight (gdw/pot)	Total culm length green (cm/pot)	Total culm length brown (cm/pot)	Total culm length (cm/pot)	Total No. of culms (pot)	Live culm wt. (gdw/pot)	Dead culm wt. (gdw/pot)	Total culm weight (gdw/pot)	Total macro-organic matter (afdg/pot)
1	1	6.0	93.0	99.0	7	0.00	7.89	7.89	0.0	0.0	0.0	0	0.00	0.00	0.00	43.44
2	1	0.0	45.0	45.0	3	0.00	10.02	10.02	0.0	0.0	0.0	0	0.00	0.00	0.00	24.55
3	1	0.0	249.0	249.0	14	0.00	7.75	7.75	32.5	0.0	32.5	1	0.22	0.00	0.22	22.18
4	1	0.0	97.5	97.5	8	0.00	4.31	4.31	0.0	0.0	0.0	0	0.0	0.0	0.0	51.13
5	1	0.0	55.5	55.5	6	0.00	3.10	3.10	0.0	0.0	0.0	0	0.0	0.0	0.0	32.65
6	1	0.0	67.5	67.5	8	0.00	5.77	5.77	0.0	0.0	0.0	0	0.0	0.0	0.0	48.62
7	2	123.5	293.5	417.0	12	0.99	8.62	9.61	111.0	52.0	163.0	5	2.88	0.51	3.39	61.98
8	2	0.0	0.0	0.0	0	0.00	0.00	0.00	260.5	32.5	293.0	13	6.20	8.69	14.89	32.97
9	2	0.0	51.5	51.5	1	0.00	0.96	0.96	353.0	30.0	383.0	17	7.33	0.00	7.33	48.61
10	2	0.0	0.0	0.0	0	0.00	2.99	2.99	446.5	7.0	453.5	21	11.94	0.34	12.28	84.96
11	2	0.0	0.0	0.0	0	0.00	1.14	1.14	250.5	0.0	250.5	10	5.26	0.04	5.30	40.64
12	2	0.0	0.0	0.0	0	0.00	7.40	7.40	331.0	24.0	355.0	19	5.37	0.70	6.07	67.51
13	3	362.5	490.5	853.0	19	5.10	11.52	16.62	297.5	15.5	313.0	15	5.16	1.07	6.23	61.46
14	3	485.5	643.5	1129.0	26	7.20	4.72	11.92	231.5	0.0	231.5	8	4.78	0.00	4.78	86.10
15	3	248.0	861.0	1109.0	21	4.91	11.02	15.93	321.5	64.0	385.5	15	7.17	4.05	11.22	55.07
16	3	136.0	484.0	620.0	24	1.98	5.55	7.53	202.0	0.0	202.0	8	7.02	0.00	7.02	70.66
17	3	0.0	22.5	22.5	2	0.00	2.82	2.82	406.0	24.0	430.0	13	11.25	1.99	13.24	65.58
18	3	107.0	72.5	179.5	4	1.14	0.86	2.00	412.0	0.0	412.0	12	19.06	3.52	22.58	85.68